

**UNIVERSIDADE FEDERAL DE SÃO CARLOS
CENTRO DE CIÊNCIAS BIOLÓGICAS E DA SAÚDE
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E RECURSOS NATURAIS**

**DISTRIBUIÇÃO VEGETAL AO LONGO DOS GRADIENTES AMBIENTAIS DE UM
ESTUÁRIO IRREGULAR**

JOSE PEDRO NEPOMUCENO RIBEIRO

SÃO CARLOS – SP

2011

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Tese apresentada ao Programa de Pós-Graduação em Ecologia e Recursos Naturais do Centro de Ciências Biológicas e da Saúde da Universidade Federal de São Carlos – São Paulo, como parte dos requisitos para a obtenção do título de Doutor em Ciências, área de concentração: Ecologia e Recursos Naturais.

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RESUMO GERAL

RESUMO

Estuário é o ambiente de mistura da água doce de um rio à água salgada vinda de um mar ou oceano. Quando essa ligação é permanente (estuários regulares), essa mistura acontece ininterruptamente, estando assim intimamente relacionada aos ciclos da maré. Em alguns estuários a conexão com o oceano é selada por uma barra de areia (estuários irregulares). Nesses casos, a mistura das águas só acontece quando essa barra se rompe, e a influência da maré é limitada. Assim, os estuários apresentam um gradiente ambiental que vai desde condições muito próximas às fluviais até quase marinhas. Nesse gradiente, a salinidade e os ciclos de alagamento são os fatores abióticos mais importantes para a distribuição das comunidades vegetais. A maioria dos estudos relacionados à distribuição vegetal em estuários foi realizada em médias e altas latitudes do Hemisfério Norte. Esses estudos apontam para uma demanda conflitante entre tolerância aos estresses ambientais e habilidades competitivas. Estuários irregulares tropicais são sob muitos aspectos diferentes, e não se sabe até que ponto as informações obtidas nos estuários regulares do Hemisfério Norte possam ser extrapoladas para os ambientes tropicais irregulares. O estuário do Rio Massaguaçu, onde esse trabalho foi realizado, é um estuário irregular. Sua barra se abre várias vezes por ano, em intervalos irregulares. O tempo em que a barra permanece aberta também é imprevisível, podendo durar desde um ciclo de maré até mais de 15 dias. Este trabalho é composto de cinco capítulos desenhados para responder questões relacionadas aos padrões e mecanismos que regem a distribuição vegetal no estuário do Rio Massaguaçu. No primeiro, criamos modelos hidrológicos para diferentes níveis da água do estuário no momento da abertura da barra e a partir deles propusemos possíveis cenários de distribuição vegetal. No segundo, determinamos os padrões de distribuição vegetal ao longo dos gradientes ambientais, e demonstramos que a importância do ambiente para a distribuição das plantas diminui junto com a salinidade, e que existe uma co-ocorrência de espécies mais intensa em trechos intermediários do gradiente. No terceiro calculamos a diversidade funcional do ambiente e mostramos que o alagamento é o principal fator abiótico na sua determinação. No quarto trabalho, apresentamos a auto-ecologia de *Crinum americanum* L., que é a espécie dominante no estuário. No quinto, mostramos como a espécie *Ludwigia octovalvis* (Jacq.) P.H.Raven responde a diferentes tempos de alagamento e como essa resposta está relacionada com a sua distribuição temporal e espacial no estuário. Estuários tropicais irregulares são ambientes pouco estudados e, embora cada um desses trabalhos tenha contribuído para nossa compreensão sobre o Estuário do Rio Massaguaçu, é importante que estudos desse tipo sejam replicados em outros estuários para que possamos entender os processos nesse tipo de ambiente. *Palavras chave: alagamento, auto-ecologia, batimetria, competição, distribuição vegetal, diversidade funcional, estresse, interações bióticas, maré, salinidade, submersão.*

INTRODUÇÃO GERAL

INTRODUÇÃO GERAL

Estuários

Estuário é o ambiente de mistura da água doce de um rio à água salgada vinda de um mar ou oceano. Esse ambiente começa no limite da influência da água salgada sobre a água doce e termina no limite da influência da água doce sobre a água salgada (WOLANSKI, 2007). Quando existe uma ligação permanente entre o rio e o oceano (estuários regulares), essa mistura acontece ininterruptamente, estando assim intimamente relacionada com os ciclos da maré. Alguns estuários têm a sua conexão com o oceano adjacente selada por uma barra de areia construída pelo próprio oceano: são os estuários irregulares¹ (MIRANDA *et al.*, 2002). Nesses casos, a mistura das águas só acontece quando essa barra se rompe, e a influência da maré é limitada (WOLANSKI, 2007). A frequência e duração dos ciclos de rompimento da barra são bastante variáveis, mas, em geral, estão relacionadas à estação chuvosa. Em casos menos frequentes a barra pode se abrir uma vez em vários anos ou várias vezes por ano.

Assim, os estuários apresentam um gradiente ambiental que vai desde condições muito próximas às fluviais, até condições quase marinhas. Nesse gradiente, a salinidade e os ciclos de alagamento são os fatores abióticos mais importantes para a distribuição das comunidades vegetais (TOUCHETTE, 2006; GREENWOOD e MACFARLANE, 2008). O sal, dependendo da concentração, pode criar uma série de disfunções fisiológicas que limitam ou impedem o crescimento vegetativo e reprodutivo da maioria das espécies vegetais (RAVEN *et al.*, 1996; KOZLOWSKI, 1997). O alagamento desencadeia uma série de alterações físicas, químicas e biológicas que alteram a capacidade do solo suportar o crescimento dos vegetais (KOZLOWSKI, 1997) e a distribuição vegetal, em ambientes alagáveis, é determinado principalmente pela frequência e duração dos ciclos de alagamento (KOZLOWSKI, 1997; SORELL *et al.*, 2002; JACKSON e COLMER, 2005). Assim sendo, a distribuição vegetal em estuários é principalmente dependente da maneira, da intensidade, da duração e da frequência dos ciclos de mistura da água do rio à água do oceano.

A maioria dos estudos, relacionada à distribuição vegetal em gradientes ambientais estuarinos, foi realizada em estuários regulares em médias e altas latitudes do Hemisfério Norte. Esses estudos apontam para uma demanda conflitante (*trade-off*) entre tolerância aos estresses ambientais e habilidades competitivas (COSTA *et al.*, 2003; PENNINGGS *et al.*, 2005), onde as espécies mais competitivas ocupariam os trechos menos estressantes e deslocariam as menos

¹ Alguns autores utilizam o termo “estuário cego”.

competitivas para os trechos mais estressantes (CRAIN *et al.*, 2004). Em estuários regulares, a previsibilidade dos ciclos da maré leva a um padrão de distribuição nas plantas caracterizado por faixas estreitas de ocorrência das espécies dominantes e baixa sobreposição de nichos (VINCE e ALLISON, 1984; PENNINGS e CALLAWAY, 1992). Em estuários irregulares, a frequência e duração da influência da maré são imprevisíveis, o que impede que o balanço competitivo seja atingido, e leva as espécies a apresentarem faixas mais largas de ocorrência, e assim, uma maior sobreposição de nichos (RUSSELL *et al.*, 1985; BALDWIN e MENDELSSOHN, 1998; COSTA *et al.*, 2003). Além disso, nos trópicos, principalmente nos estuários irregulares, onde a influência da maré é limitada, a importância relativa da chuva é muito maior. Dessa maneira, não se sabe até que ponto as informações obtidas nos estuários regulares do hemisfério norte podem ser extrapoladas para os estuários tropicais irregulares (COSTA *et al.*, 2003). A distribuição vegetal em gradientes ambientais é uma das maiores lacunas no nosso conhecimento sobre ambientes estuarinos, e a sua compreensão é fundamental para sua conservação e restauração (CRAIN *et al.*, 2004).

A planície costeira é historicamente a parte mais populosa da Terra. Os estuários e a plataforma continental correspondem a pouco mais de 5% da superfície da Terra, mas abrigam cerca de 60% da população humana (LINDEBOOM, 2002), e são responsáveis por 90% do que é pescado no mundo (WOLANSKI *et al.*, 2004). Entre as maiores cidades do mundo 60% se localizam às margens de um estuário (MIRANDA *et al.*, 2002), e hoje esses ambiente sofrem os mais diversos tipos de impactos, que vão desde contaminação por metais pesados até sobre-pesca (veja WOLANSKI *et al.*, 2004). Além disso, frequentemente, a avaliação dos impactos causados pelo manejo hidrológico dos rios sobre os estuários é negligenciada. Assim, todo o impacto sobre os ambientes estuarinos e conseqüentemente sobre a pesca e a população costeira é tido como conseqüência inevitável do desenvolvimento das áreas a montante (WOLANSKI *et al.*, 2004). Existe assim uma grande demanda pelo avanço do conhecimento sobre esse tipo de ambiente, e da integração desse conhecimento no manejo das bacias hidrográficas. Nesse sentido, a nossa capacidade de entender o ambiente e de propor modelos preditivos sobre ele precisa ser significativamente melhorada (veja SMITH, 2000).

Estuário do Rio Massaguaçu

O estuário do Rio Massaguaçu² (Caraguatatuba, SP, Brasil - 23°37'20''S e 54°21'25''O) é um estuário irregular. Ele está localizado em uma região de clima tropical úmido (af), com invernos amenos, chuvas em todos os meses do ano, e sem uma estação biologicamente

² Recentemente a prefeitura mudou o nome do Rio Massaguaçu para Rio Capricórnio. Não conseguimos determinar o caráter dessa alteração, assim, adotamos nesse trabalho o nome antigo, que consta nos mapas do IBGE.

seca definida (Köppen 1940). Sua margem direita é um fragmento de floresta ombrófila densa e elementos de floresta de restinga, em diversos graus de conservação. A margem direita é um cordão de areia, que hoje está bastante antropizado. Esse cordão, entretanto, ainda apresenta a vegetação ripária em quase toda a sua extensão (figura 1).



Figura 1. Localização regional e imagem aérea do Estuário do Rio Massaguaçu. No detalhe, o estuário com a barra fechada e aberta. As letras indicam a localização aproximada dos bancos de macrófitas. Fonte: Google Earth.

Esse estuário possui cinco grandes bancos de macrófitas, ocupados por densas formações de plantas aquáticas e anfíbias. Eles ficam totalmente expostos quando a barra de areia está aberta, e totalmente submersos (com exceção das árvores e do ápice de algumas espécies de macrófitas) quando o estuário está próximo do seu nível máximo. Fora dos bancos, o assoalho do estuário é de areia, não apresenta vegetação e está quase todo o tempo submerso. Os bancos estão localizados longitudinalmente no estuário, e oferecem assim um ambiente propício para o estudo da distribuição vegetal tanto ao longo do seu eixo horizontal (principalmente salinidade) quanto vertical (principalmente o alagamento).

A barra do Estuário do Rio Massaguaçu se abre várias vezes por ano. Assim, diferentemente do que acontece com a maioria dos estuários irregulares, a abertura da sua barra não parece estar relacionada a nenhuma estação do ano. O intervalo entre uma abertura e outra é bastante variável, indo de poucos dias até mais de um mês. O tempo em que a barra permanece aberta também é imprevisível, variando desde um ciclo de maré até mais de 15 dias. Os ciclos de abertura são eventos naturais, frutos principalmente da combinação da força e altura das marés (e conseqüentemente do tamanho e altura da barra) e da quantidade de água despejada pelo rio e pela chuva (e conseqüentemente nível do estuário). A abertura da barra leva a uma drástica redução do volume da água e posteriormente à entrada de água salgada no sistema, o que causa alterações profundas nas condições químicas, físicas e biológicas do ambiente (SUZUKI *et al.*, 2002)(figura 2).

Infelizmente, abertura artificial de barras de areia de estuários irregulares é uma prática comum no litoral brasileiro (SUZUKI *et al.*, 2002; SANTOS *et al.*, 2006; BRANCO *et al.*, 2007; RIBEIRO, 2007). No estuário do Rio Massaguaçu, essa abertura era realizada, tradicionalmente, por agricultores, quando o estuário começava a alagar as plantações. Depois, passou a ser aberta por pescadores, para facilitar a captura de pescados, e depois por surfistas, uma vez que o processo de abertura torna a praia propícia para a prática do esporte. Nos últimos anos, a prefeitura também começou a abrir artificialmente a barra (veja escavadeira na Figura 2), com a justificativa de evitar alagamento nos bairros a montante. Essa abertura, entretanto, está acontecendo de maneira cada vez mais frequente, com o estuário apresentando níveis cada vez mais baixos. Não existe nenhum controle ou estudo sobre o impacto dessa prática sobre o estuário e, em geral, a decisão de abrir a barra é tomada pelo operador da escavadeira, sem nenhum conhecimento oficial da prefeitura ou qualquer embasamento teórico. Existe assim uma demanda muito grande por estudos relacionados aos ciclos de abertura de barra e seus efeitos sobre a comunidade estuarina, para que o manejo, quando necessário, seja feito de maneira adequada (veja SUZUKI *et al.*, 2002).

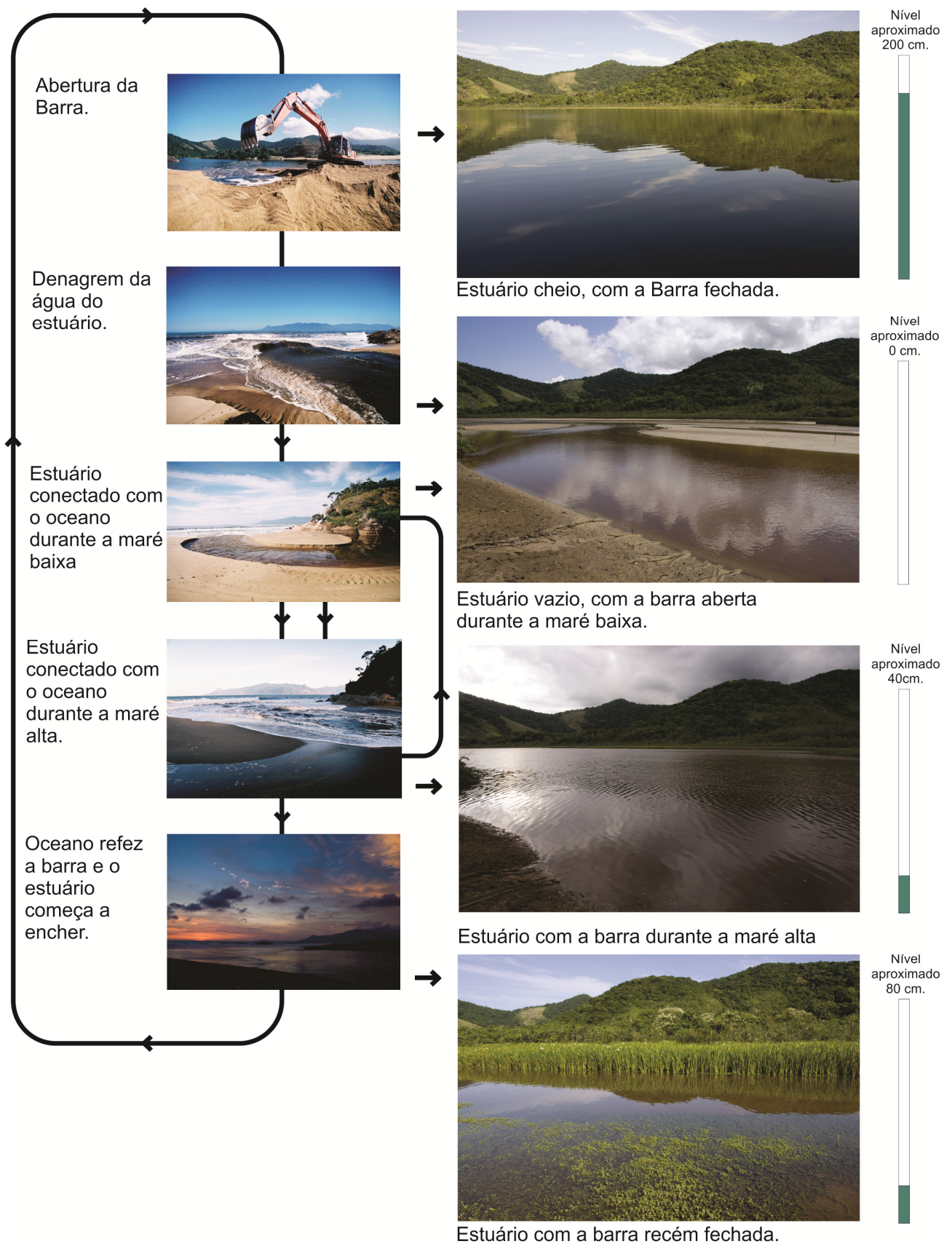


Figura 2. Ciclo de abertura de barra do Estuário do Rio Massaguaçu.

Ecologia do Estuário do Rio Massaguaçu

Esse trabalho faz parte de um projeto maior do Laboratório de Sistemática e Ecologia Química do Departamento de Botânica da Universidade Federal de São Carlos chamado: “Florística, Fitossociologia e Ecologia Química do Estuário do Rio Massaguaçu” (veja RIBEIRO, 2007; MATSUMOTO, 2009; RIBEIRO *et al.*, 2009; TAKAO, 2010). Até onde sabemos, não existe nenhum outro estudo de cunho ecológico na região.

Este trabalho é dividido em cinco capítulos, que tentam responder questões relacionadas aos padrões de distribuição e funcionamento da comunidade vegetal e aos ciclos hidrológicos em um estuário tropical irregular. No Capítulo 1, determinamos as características hidrológicas do estuário e, a partir delas, propusemos um modelo preditivo dos ciclos de abertura e fechamento de barra. Baseado no manejo artificial da barra, usamos esse modelo para apresentar e discutir cenários futuros. No capítulo 2, determinamos os padrões de distribuição vegetal ao longo desse ambiente e discutimos a importância relativa do ambiente e das interações competitivas para o estabelecimento desses padrões. No Capítulo 3, calculamos a diversidade funcional de diferentes trechos do estuário e determinamos qual a relação dos valores de diversidade com as variáveis ambientais ao longo do gradiente. No Capítulo 4, apresentamos a auto-ecologia de *Crinum americanum* L., que é a espécie dominante no estuário. No Capítulo 5, mostramos como a espécie *Ludwigia octovalvis* (Jacq.) P.H.Raven responde a diferentes tempos de alagamento, e como essa resposta está relacionada com a sua distribuição temporal e espacial no estuário.

Outros trabalhos

Durante o período de doutorado eu realizei alguns trabalhos paralelos. Por uma questão de coesão resolvemos publicá-los como artigos independentes. Assim, eles não fazem parte do corpo dessa tese, mas são apresentados brevemente nesse tópico.

Global Effect Index: a New Approach to Analyzing Allelopathy Surveys Data. Neste trabalho proponho uma nova maneira de se analisar dados provenientes de bioensaios de alelopatia. A ideia é que, através da combinação dos valores obtidos para cada um dos parâmetros (tempo médio de germinação, porcentagem de germinação, tamanho da plântula etc.) é possível gerar um índice que represente melhor os efeitos globais de uma planta doadora sobre uma receptora do que a análise separada de cada um dos parâmetros (RIBEIRO, 2011).

Potencial alelopático de Crinum americanum L. sob diferentes condições de extração. Neste trabalho testamos diversas maneiras de se extrair os aleloquímicos de folhas secas de *C.*

americanum, no sentido de obter a maior efeito inibitório possível a partir de uma dada quantidade de material botânico (RIBEIRO e LIMA, no prelo-b).

Allelopathic effects of orange (Citrus sinensis L.) peel essential oil. Nesse trabalho determinamos o potencial alelopático do óleo essencial de laranja sobre o crescimento inicial de espécies invasoras de cultura (RIBEIRO e LIMA, no prelo-a).

Mammalia, Carnivora, Mustelidae, Lontra longicaudis Olfers, 1818: Occurrence record in an estuary area in the state of São Paulo, Brazil. Durante o esforço de campo do presente trabalho, frequentemente encontrávamos fezes e pegadas de lontra. Mais raramente, era possível avistar o animal. Em janeiro de 2010 finalmente conseguimos registrar em foto um exemplar no estuário. Esse artigo é o registro formal dessa ocorrência (RIBEIRO e MIOTO, 2010).

Aquatic, amphibian, and marginal flora of an irregular estuary, Caraguatatuba, state of São Paulo, Southeastern Brazil. Embora as discussões ecológicas dessa tese se baseiem nas espécies principais do estuário, durante o campo coletamos um número muito maior de espécies. Para que o inventário completo da flora fosse tornado público, unimos a lista completa de espécies à lista proveniente de um levantamento da vegetação ripária (que realizamos em outro trabalho) e submetemos a uma revista especializada em listas de espécies (RIBEIRO *et al.*, 2011).

The role of allelopathy in controlling weeds through crop rotation. Diversas plantas do estuário do Rio Massaguaçu apresentam forte potencial alelopático. Assim, o projeto original previa a realização de experimentos relacionados ao tema. Isso faria um paralelo entre o conhecimento ecológico do ambiente e as possibilidades do seu uso aplicado. Alguns experimentos chegaram a ser feitos (RIBEIRO, 2011; RIBEIRO e LIMA, no prelo-b), mas a parte principal realizar-se-ia durante a realização de um Doutorado Sanduíche (Doutorado Sanduíche, CAPES processo 0033-10-3). A idéia era realizar uma parte experimental e entrar em contato com novas técnicas na *University of New England*, Armidale, Austrália, e aplicar essas técnicas em experimentos no Brasil. Infelizmente, o processo de obtenção do visto para a entrada na Austrália demorou mais de cinco meses do que o prazo previsto. Isso atrasou consideravelmente a viagem, e não deixou tempo hábil para a realização de experimentos no Brasil. Outro entrave foi que o IBAMA negou o pedido de licença de transito do material botânico (Requerimento: 109427), o que impossibilitou que a parte experimental do período do Doutorado Sanduíche fosse realizada com plantas do estuário do Rio Massaguaçu. Acreditando que a importância de trazer novas técnicas e novas visões para o Brasil ser justificável por si só, o Doutorado Sanduíche foi mantido. Entretanto, tema do manuscrito gerado ficou completamente descolado do foco central dessa tese.

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CAPÍTULO 1

The effects of artificial sandbar breaching on an irregular estuary community³.

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Abstract

Artificial sandbar opening of irregular estuaries is a world-wide practice to improve water quality, fishing, recreational amenity, and to prevent flooding of adjacent property. The breach causes the water level to drop drastically, and exposes plants to two extremes of water supply. With few exceptions, estuarine community is adversely affected by this practice. Although natural events, artificial breaching is on the increase, and there is a demand for understanding the impacts on water level manipulation on estuarine community. In this work we described breaching cycles for Massaguaçu River Estuary and based on that, proposed flooding scenarios for the estuary macrophytes banks. We calculated the relationships between plant distribution and flooding condition, and from that, predicted estuary community on different water levels at breaching time. We found strong relationships between plant distribution and flooding condition, and we expected estuary community to be marked different between flooding scenarios. Therefore, we concluded that the artificial increase of breaching cycles have detrimental effects on estuary community.

Key words: conservation, estuarine plants, flooding, tide, water level.

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1. Introduction

In irregular estuaries, the connection with the ocean is sealed by a sandbar. This barrier naturally breaches from time to time (Gladstone *et al.*, 2006), causing estuaries to drain, and leading to drastic changes in the environmental conditions (Macek *et al.*, 2006, Ribeiro *et al.*, in press, Suzuki *et al.*, 2002). Breaching cycles are usually related to the rainy season (Gladstone *et al.*, 2006, Santangelo *et al.*, 2007), but it is possible for a sandbar to breach several times throughout the year (Ribeiro *et al.*, submitted) or one time in several years (Miranda *et al.*, 2002). Artificial sandbar opening is a world-wide practice to improve water quality, fishing, recreational amenity, and to prevent flooding of adjacent property (Gladstone *et al.*, 2006, Santangelo *et al.*, 2007, Santos & Esteves, 2004). With few exceptions, estuarine community is adversely affected by the sandbar breach (Riddin & Adams, 2008, Santos *et al.*, 2006, Santos & Esteves, 2004). Biomass loss after these events can reach 99% (Anandraj *et al.*, 2008), and in some cases, community is unable to reestablish itself, suggesting little resilience to this disturbance (Santangelo *et al.*, 2007). Generally, the impact is not as dramatic, and estuarine community is able to cope with sporadic natural sandbar breaches. However, the impact of systematic man-caused breaching is unknown (Gladstone *et al.*, 2006, Ribeiro *et al.*, submitted).

Breaching cycles expose plants to two extremes of water supply (Macek *et al.*, 2006). When estuary mouth is sealed, water level is high, and plants must be able to live under submerged conditions. Submergence reduces O₂ and CO₂ availability (Jackson & Ram, 2003), leading to a reduction of the photosynthesis. Indeed, prolonged floods can have detrimental effects even on amphibious plants (Yáñez-Espinosa *et al.*, 2008). Furthermore, re-exposure after prolonged submergence can produce toxic compounds through oxidation of the flooded soil (Biemelt *et al.*, 1998). When breaching frequency is artificially increased, duration of submersion decreases. As riparian plants are usually able to cope with sporadic flooding, adjacent forest is expected to advance and displace estuarine flora to a lower level.

There are some studies regarding species response to sandbar breach in the tropics (Santos *et al.*, 2006, Santos & Esteves, 2002, Santos & Esteves, 2004, Suzuki *et al.*, 2002, Suzuki *et al.*, 1998). Generally, they reported detrimental effects on macrophytes after a breach. However, these studies focus on the effects of a given breach on a given species, and there is a demand for a predicting model for systematic breaching effects on plant community.

Massaguaçu River is an irregular tropical estuary, which sandbar has been traditionally breached. Particularly in the last few years this practice is on the increase, in order to prevent the flooding of adjacent properties. We expected that increase of breaching frequency by artificial

means will lead to detrimental effects on plant community, resulting in changes in species composition, zonation and population size. To test this hypothesis our objective in this work was to: (1) better characterize the breaching cycles, (2) create flooding conditions scenarios bases on different levels of sandbar breach, (3) determine how species are related to flooding condition, and (4) determine how species would occupy each flooding scenarios.

2. Material and methods

Study Site – The estuary of the Massaguaçu River (23°37'20''S e 54°21'25''O) is an irregular estuary. Its sandbar breaches several times every year, when the water level can decrease more than 2 m (Ribeiro et al., in press). Frequency of this event is markedly irregular, ranging from few days do more than one month. The period that estuary and ocean remain connected is also variable, and ranges from one tidal cycle, to about two weeks. Breaching cycles are natural events, and are manly related to relative high between sandbar and water level, and tidal strength. Tides are also important in determining the sandbar height, which can become strictly higher during periods of strong waves. However, Massaguaçu River estuary sandbar has been systematically open, first by fisherman and farmers, then by surfers, and more recently by the City Hall, in order to prevent flooding of adjacent propriety. To the best of or knowledge there is no formal record of this practice, but with the land use intensification, man-made breaching is becoming more frequent. The estuary presents five major macrophytes banks, in which we conducted this research (figure 1 - veja figura 1, pagina 13).

Estuary water level and sandbar breaching – We installed in the estuary a graduated scale, where 0 cm represents the lowest level estuary water reach (which occurs during the low tide when the sandbar is opened). Between June 2007 and August 2010 we made daily readings of the water level.

Floristic – We randomly chose 80 plots (5x5 m – 25 m²) in each macrophytes bank (total of 400 plots). In each plot we registered covering area and density of each species (see Ribeiro et al., in press). We also measured the relative (to the 0 cm in the graduated scale) plot high. When there was tree in the plot, we count individuals.

Hydrology – On April 2010, we performed a bathymetry in the estuary. We than interpolated the resulting data and calculate the elevation-volume curve. When the sandbar is opened, estuary and ocean are connected, and estuarine water level changes with the tide. The level in these moments ranges from 0 cm (low tide) to about 40-60 cm (high tide). After the mouth

closed, water level starts to rise independently from the tidal regime (see details in Results). Thus, using values bigger than 60 cm in the elevation-volume curve, we performed a linear regression as so to be able to predict variation in estuary volume when the sandbar is closed (figure 2).

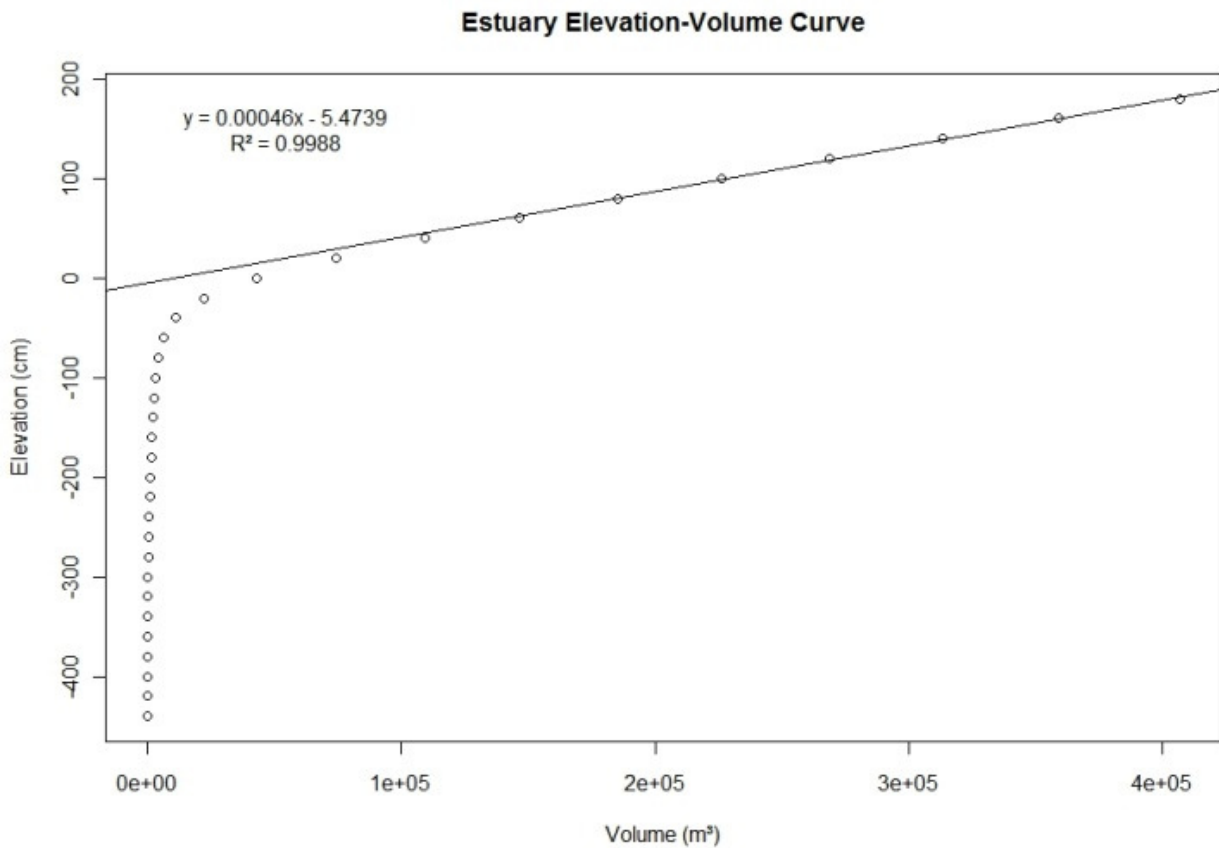


Figure 2. Estuary Elevation-Volume curve. The linear regression describes elevation-volume relationship to elevations bigger than 60 cm.

Using this regression, we calculated estuary volume in each sampled day. Subtracting the volume of a given day by the volume of the previous day we determined the volume daily retained (the balance between gains and losses, hereafter: volume added) by the estuary. We also classified the estuary water level in classes. From that, we obtained an equation that describes the volume added to the estuary according to its water level (figure 3).

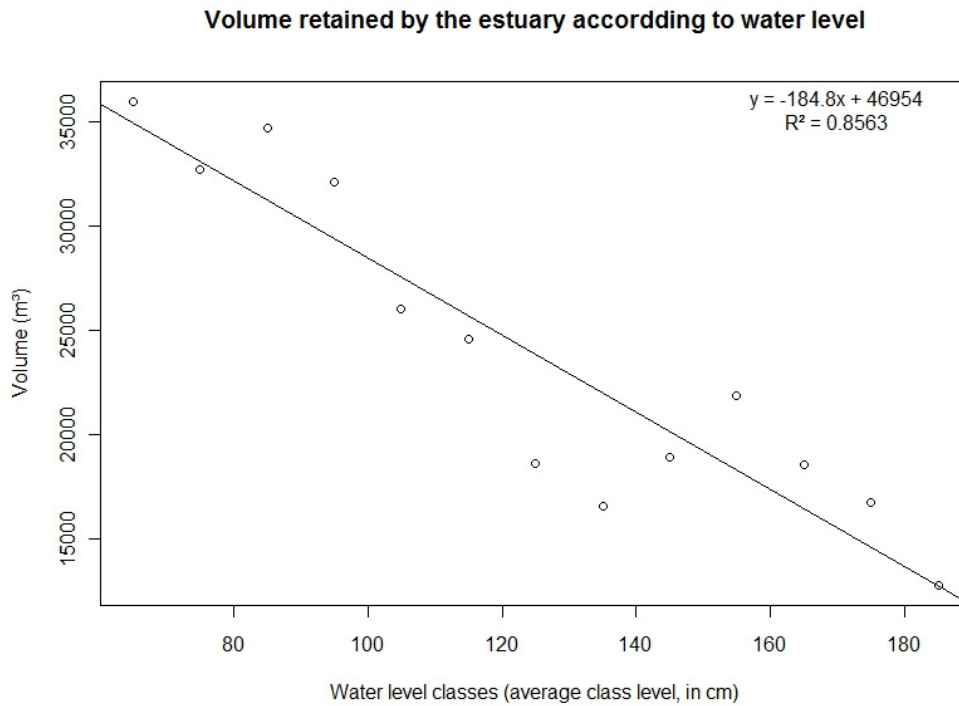


Figure 3. Relationship between estuary elevation and volume daily added.

Using the elevation-volume regression, we determined estuary volume just after a hypothetical sandbar closure (day 1). Using the volume added-water level regression, we determined the volume added to the estuary in this day. Adding this volume to day 1 volume, we determined the initial volume for day 2. Based on that volume, we calculated the estuary elevation on day 2. From that elevation we determined the volume added to estuary on day 2. Adding this volume to the initial day 2 volume, we determined the initial volume for day 3. Using this procedure we create a model hydrologic cycle for the estuary up to theoretical volume stabilization. From that cycle is possible to determine duration and characteristics of hydrologic cycles in different Estuary water level at breaching time (WLBT).

We grouped plots in elevation classes, and based on the hydrologic cycle calculated the time each class remains flooded in four WLBT scenarios: (1) 141 cm, lowest level estuary was artificially breach, (2) 190 cm, average level we estimated, based on marks on the rocks, estuary used the breach, (3) 220, highest breach level recorded and, (4) 100, hypothetical low WLBT. Additionally we calculated flooding time of plots at actual average WLBT, 165 cm.

Plant response to water level – Species usually present a clear relationship with flooding, being more abundant in a given flooding condition, and rarer in location where the flooding is more frequent or less frequent. We selected the 12 main (veja table 3, pagina 89) macrophytes species in the estuary (Whitaker plots), and based on actual species density and plots flooding time,

calculated the polynomial regression that describes the relation between each species and flooding (Figure 4)

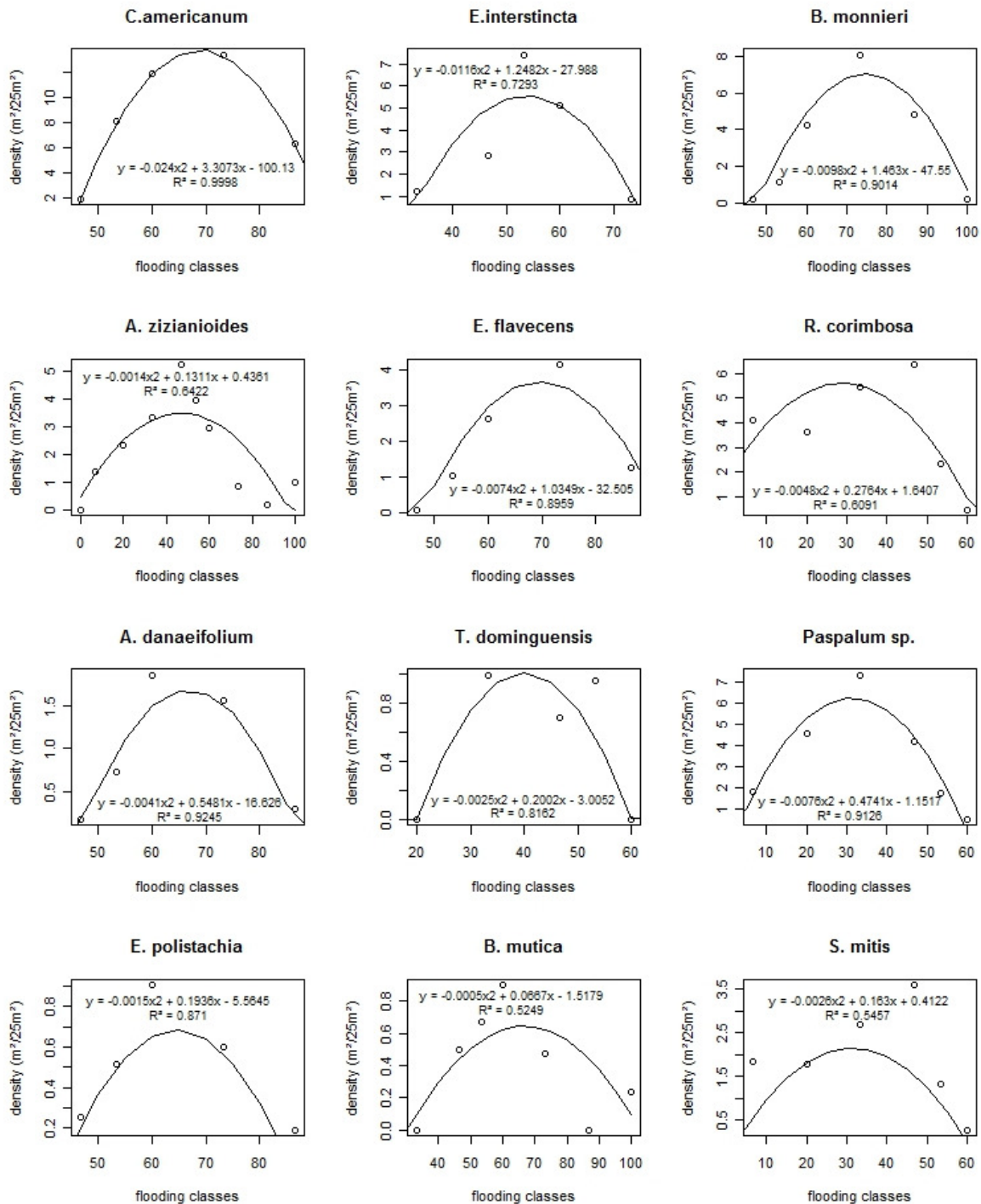


Figure 4. Relationship between species distribution (density, m²/ 25 m²) and flooding (percentage of flooding time).

Using this regression, we calculated species density to each plot in the four scenarios. We performed the same procedure for the three main tree species, and for combined presence of

trees, including all species. Besides, in order to help understand at each level estuary water actually starts to flood proprieties, we visited the spots that, according to local population, the City Hall claims to get flooded by the estuary.

3. Results

During the sampled period, estuary presented 72 breaching cycles. To the best of our knowledge, the city hall does not keep a record of when it breaches the sandbar. As we recorded estuary level, but did not monitored the sandbar itself, we were unable to determine whether the breach was natural or man-caused. However, on several occasions we saw the City Hall loader on its way to the sandbar, and estimate the man-made (City Hall and surfers) breaching in about 70% of the cases. The average WLBT was 165 cm, with a maximum of 220. The lowest man-made breaching level we recorded was 141. Natural breaching at lower WLBT just after estuary mouth closure is relatively common, as the ocean needs several days to rebuild a high bar. Based on marks on the rocks we estimated estuary breaching level in about 190 (Figure 5). This is probably not a very precise measure, but as historical water level measurements are unavailable, might give a clue of which WLBT the estuary used to have. The period that estuary and ocean remain connected ranged from one tidal cycle to 19 days, with an average of 4 days. We expected that breaches at higher water level to carries more sand to the ocean, opening bigger channels. In these cases, the ocean would take longer to rebuild the sandbar, and the duration of estuary-ocean connection would last longer. However, there were no relation between connection duration and water level when sandbar breaches (Figure 6).

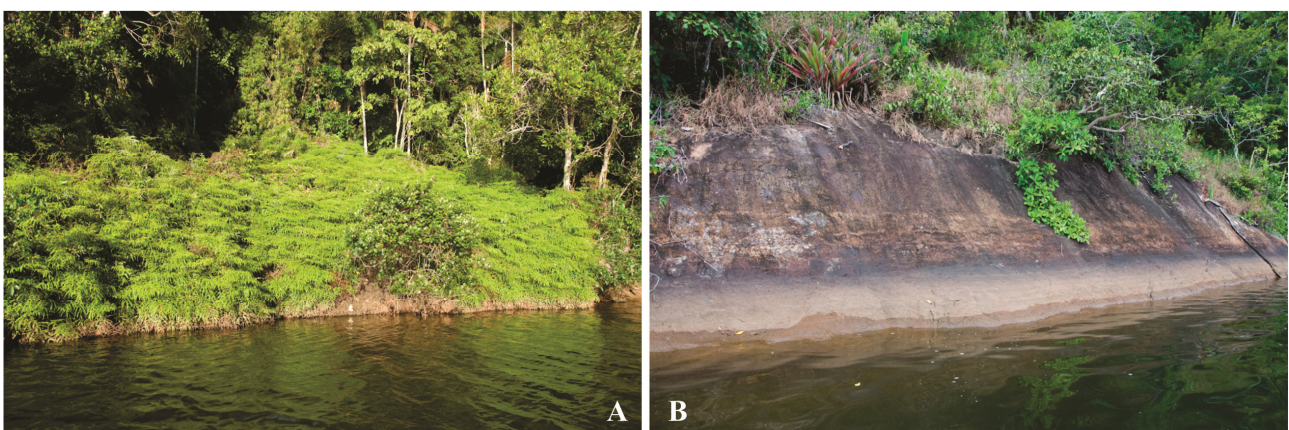


Figure 5 – Water marks on the riparian vegetations (A), showing the present average water level at breaching and (B) in rocks, showing historical water level at breaching time. Pictures takes 5 minutes apart. Precision of this estimations needs to be tested.

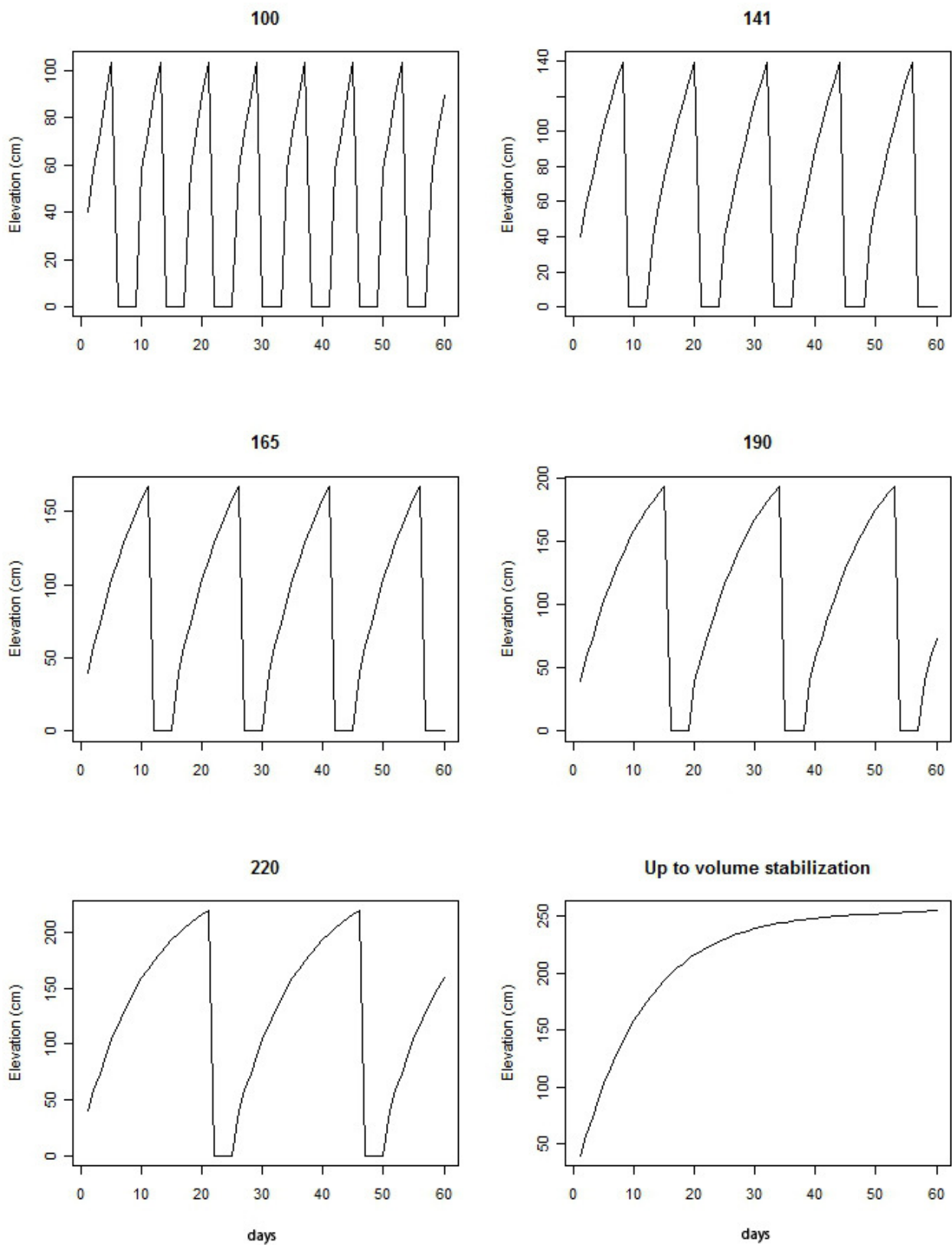


Figure 7. Theoretical breaching cycles models for different sandbar high at breaching level.

The 12 main species presented a clear relation with flooding. Therefore, their distribution in the four scenarios varies remarkably (Figure 8) Beside changes in population size, species distribution in estuary also changes (figure 9).

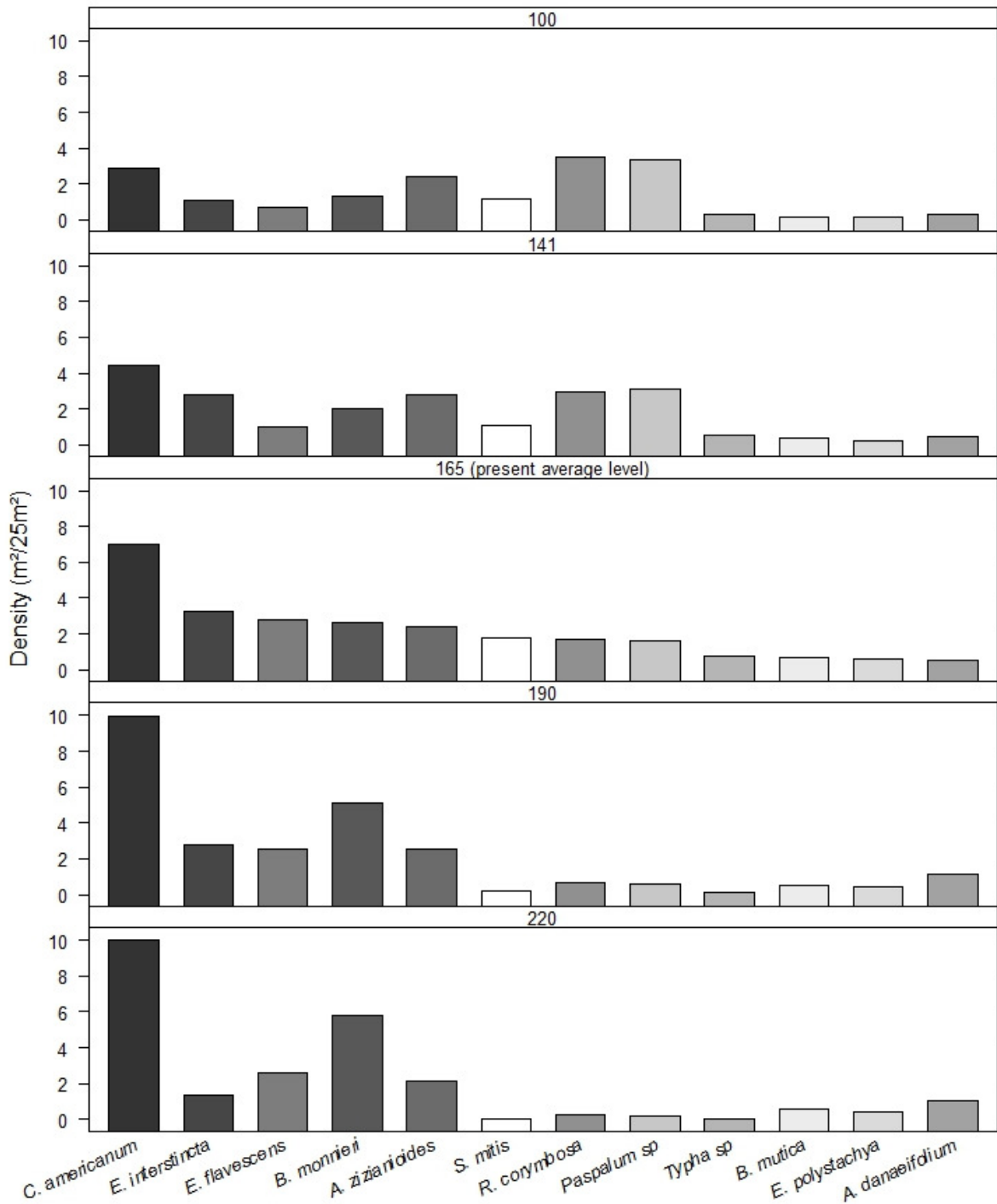


Figure 8. Twelve mains species abundance in present and theirs estimated abundance in four water level height at breach time scenarios.

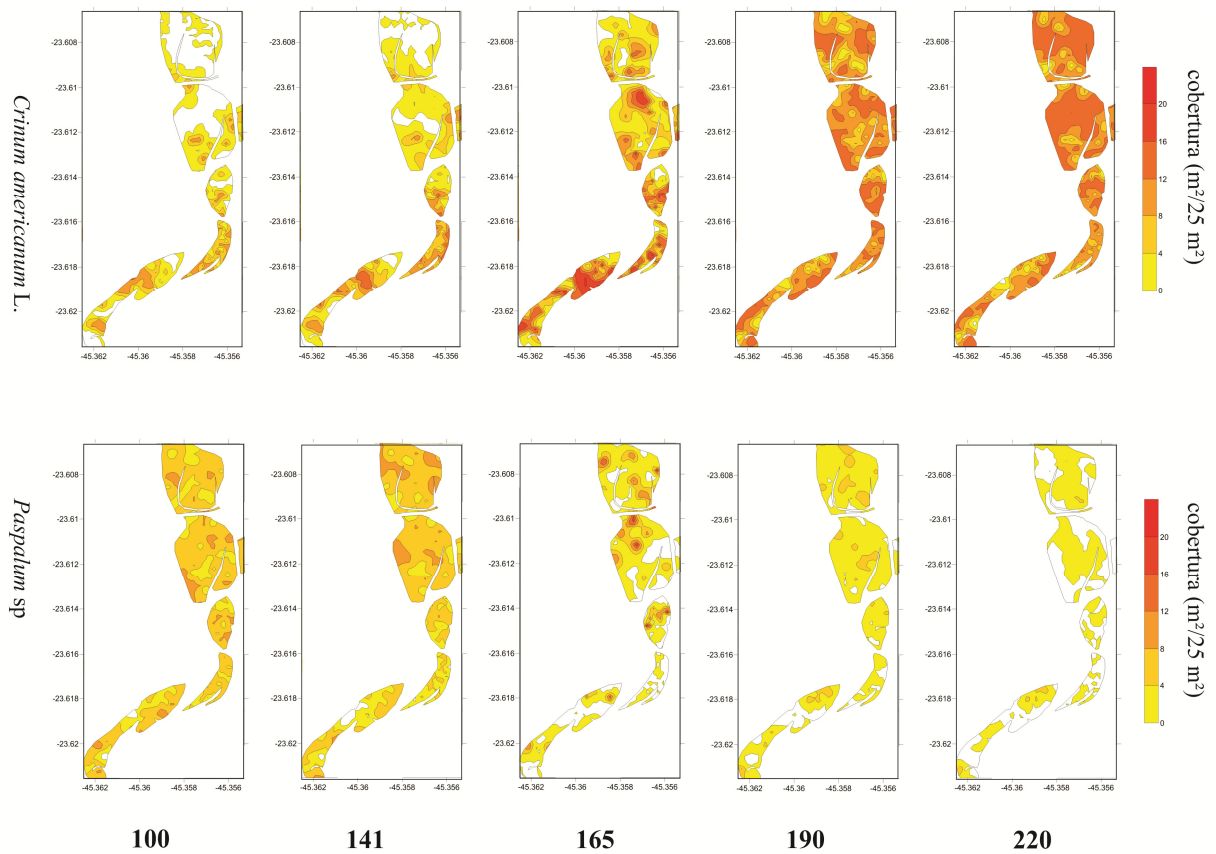


Figura 9. *Crinum americanum* and *Paspalum* sp zonation in Massaguaçu River Estuary in the five different flooding scenarios.

The three main tree species (*Annona glabra* L, *Callophylum brasiliensis* Cambess., *Tocoyena bullata* Mart.) presented a relation with flooding as well. Though trees usually occupy less flooded plots when compared to macrophytes, their presence is also very dependent of flooding cycles. Therefore, they are also sensitive to changes in water regime, and their population vary drastically between the WLBT scenarios (figure 10).

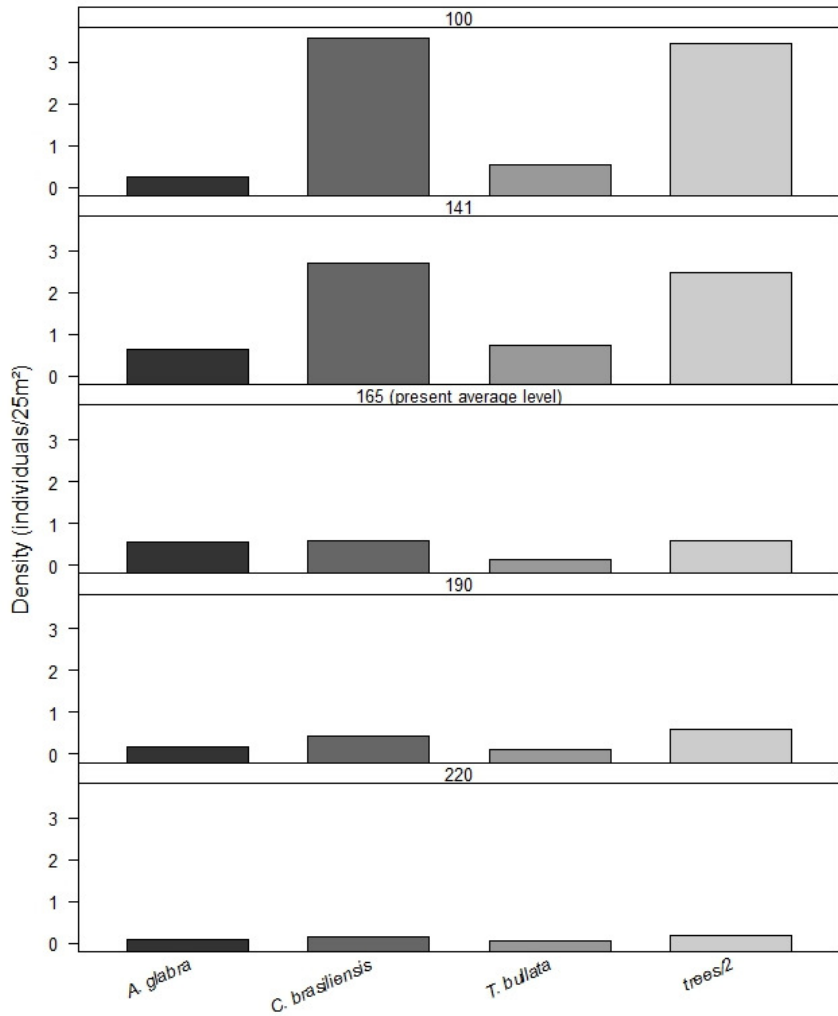


Figure 10. Three main tree species abundance in present and their estimated abundance in four sandbar height at breach time scenarios. Tree presence, regardless of species is also presented (n/2, to fit graph).

4. Discussion

Plant zonation in estuaries are mainly controlled by species capacity of coping with environmental stress and to their competitive abilities (Crain *et al.*, 2004, Greenwood & MacFarlane, 2008). As proposed scenarios disregard biotic interactions and abiotic drivers other than flooding, one must remember that its predictiveness is limited to a certain extent. In the other hand, flooding is, along with salinity, the main abiotic driver for plant distribution in estuarine environments (Bockelmann *et al.*, 2002, Costa *et al.*, 2003, Silvestri *et al.*, 2005). Indeed, plants distribution in Massaguaçu River Estuary presented clear relation with flooding. Thus, results in

this work are likely to help understanding the impacts caused on estuary community by water level manipulation.

Although tolerance to different flooding conditions varies, distribution of the main species is closely related to plot flooding condition. Thus, changes in estuary hydrological cycles are expected to lead to changes in plant assemblage. For example, *Crinum americanum* L. is a species that is tolerant to environmental stress and at the same time, and aggressive competitor (Ribeiro et al., in press). At present WLBT this species is by far the most abundant in estuary. At 100 WLBT scenario this species is expected to lose near half of its population, and although remains an abundant species, will not be the most abundant one. Correspondently, at 100 WLBT scenario *Paspalum* sp. population is expected to triple when compared to the present, and became the most abundant species. In the other hand, at 220 WLBT the populations of species related to less flooded plots, such as *Sleria mitis* and *Paspalum* sp. are expected to be drastically reduced. Tree species responds similarly to changes in flood conditions. As they are related to less flooded plots than macrophytes, generally tree presence are expected to increase in lower WLBT, and decrease at higher one. Tree presence is expected to be almost null at 220 WLBT.

Changes in size and zonation on the population of each species may lead to great changes in plant assemblages. Thus, estuary water level manipulation can result in drastic changes in estuarine community. Higher WLBT leads to a very stressing flooding condition, with prolonged periods of soil waterlogging and biomass submersion. Still, toxic compounds can be produced in soil re-exposure after prolonged submergence (Biemelt *et al.*, 1998). Besides, higher WLBT usually produces strong breaching, that represents a mechanical stress. Thus, plant community is expected to be dominated by a few species adapted to cope with this condition. Lower WLBT are characterized by sporadic short duration flooding. During very low WLBT plants may not experience photosynthetic tissues submersion, and breaching does not impose a mechanical stress. As most terrestrial species can withstand sporadic flooding, plant assemblages in low WLBT conditions are expected to present more species and bigger equitability.

Other Species – Massaguaçu River Estuary presented 51 macrophytes species. While the 12 main species represents over than 90% of macrophytes covering in the estuary, the other 39 represents less than 10%. The impact we predict to the main species are likely to happen to most all other estuarine species. In small populations, impacts of artificial sandbar can be as dramatic as species exclusion. Exclusion is likely to happen with small population of species exclusive of very flooded plots, such as, *Eleocharis minima* Kunth, or rarely flooded plots, as *Calyptracarya longifolia* (Rudge) Kunth. Thus, while changes in 12 main species are only quantitative, changes in

species related to extremities of flooding condition can be qualitative, and species richness can varies within different WLBT.

Associated fauna – Impacted on macrophytes communities will inevitably lead to impacts on its associated fauna. To Massaguaçu River Estuary the only work regarding that matter we are aware of related several species of macroinvertebrates living in association with *C. americanum* (Hanashiro et al, unpublished data). The nature of this association still requires investigations (as does for associated fauna of all plants in the estuary). However, changes in *C. americanum* populations are very likely to lead to changes in the population of these species.

Fish mortality – Sandbar breaching to increase fishery is a common practice, as several commercial fish uses estuaries for feeding and reproduction. The effects of this practice on other species are usually not taken into account, and little is known about systematic breaching on fish community. While doing this survey we noticed a great number of occasional puddle created by water level decrease. These puddles trap a great number of fish, which usually died. Besides, we expected estuarine fish to be carried to the ocean by flowing water during the breach. Thus, while these events naturally interfere in fish population, systematic breaching can became a treat to some species. These hypothesis needs to be tested.

Otter – The Massaguaçu River estuary shelters a small population of river otters (*Lontra longicaudis*, Olfers, 1818)(Ribeiro & Mioto, 2010). This specie is data deficient according to IUCN red list (IUCN, 2009), and there is no studies of direct and indirect impacts of artificial sandbar breaching on this species.

Riparian forest - The more WLBT is reduced, the less the higher plots will be flooded. With flooding stress reduction, it is plausible to expect the riparian forest to replace macrophytes assemblages. Accordantly, higher WLBT will lead to frequent and prolonged flooding conditions in higher plots, and riparian trees, adapted to cope with sporadic flooding are expected to be replaced to amphibians trees or macrophytes.

Adjacent propriety flooding and conservation – When the sandbar is well above estuary level or during strong waves, shovel breaching is almost impossible. Thus, even thought surfer and fishers can increase breaching cycles, their action is limited to certain conditions, usually when estuary level is above 160 cm, waves are weak, during low tides. In the other hand, the City Hall loader can breach the sandbar at virtually any conditions. This is a growing treat, as breaching in very low water levels is happens more often. During lowest level city hall breached the sandbar, 141 (there was several breaches little above that) part of macrophytes banks still exposed. In one

occasion when estuary water level was 212 cm, we visited all points that are claimed to be flooding by estuary during high water levels. None of these points were flooding, and some of them were way before that happens. The lower point was about 40 cm above water level, which suggest estuary water level can be as high as 250 cm without being a flooding treat. Although a study addressed specifically to determine at which water level estuary really needs to be breached, this suggests that estuary sandbar has been breached way before it is actually needed.

5. Acknowledgments

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CAPÍTULO 2

Plant zonation in an irregular estuary: the relative importance of environment and competition.⁴

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Running headline: Plant zonation in an estuary

Abstract

Estuaries present an environmental gradient that ranges from almost fresh water conditions to almost marine conditions. Salinity and flooding are the main abiotic drivers for plants. Therefore, plant zonation in estuaries is closely related to the tidal cycles. It is expected that the competitive abilities would be inversely related to the tolerance towards environmental stress. Thus, in estuaries

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the plant zonation tends to be controlled by the environment near the sandbar, and by competitions away from it. This zonation pattern was proposed for regular non tropical estuaries. For tropical estuaries the relative importance of the rain is higher, and it is not clear to what extent this model can be extrapolated. We measured the tidal influence along the environmental gradient of a tropical irregular estuary, and quantified the relative importance of the environment and the competition interaction along this gradient. Contrary to the thin occurrence zone that would be expected for regular estuaries, plants in tropical estuaries presented large occurrence zones. However, the relative importance of the environment and competition showed in this study followed the same patterns proposed for regular estuaries. The environmental unpredictability allows the plants from to occur in larger zones, but these zones arise from occasional spots, and most species populations are concentrated in relatively thin zone.

Key words: biotic interactions; distribution pattern; salt, soil waterlogging; tidal environments

1. Introduction

Estuaries are the mixture environment of a river freshwater to an ocean saltwater. When river and ocean are permanently connected (regular estuaries), the water mixture occurs in a continuum, and therefore, are closely related to the tidal cycles. Sometimes, the ocean builds a sandbar that seals its connection to the river (irregular estuaries). In these cases, the water mixture only happens when the sandbar breaches, and tidal influence is limited (Wolanski, 2007). Estuaries are delimited by saltwater influence over the freshwater in one extremity, and by the freshwater influence over the saltwater on the other. Therefore, estuaries present an environmental gradient that ranges from almost freshwater conditions to almost marine conditions (King et al., 1990; Pennings and Callaway, 1992; Wolanski, 2007). In this gradient, salinity and flooding cycles are the main abiotic drivers for plant community zonation (Touchette, 2006; Greenwood and MacFarlane,

2008). In non halophytes plants, salt can lead to ionic toxicity, hormonal disturbance or both (Raven et al., 1996). Flooding unchains a series of physical, chemical and biological changes in the soil, that completely modify its ability to support plant growth (Kozlowski, 1997), and plant zonation in flooding areas is closely related to the water level (Sorell et al., 2002). Therefore, the plant zonation in tidal environments is mainly dependent upon the salinity and flooding cycles (Costa et al., 2003; Greenwood and MacFarlane, 2008).

Plant distribution and abundance along estuaries are indicative of its tolerance towards the environmental drives and its competitive abilities (Crain et al., 2004; Pennings et al., 2005; Greenwood and MacFarlane, 2008). In harsh environments, the ability to cope with abiotic stress tends to be more important to plant zonation, while in benign environments the competitive abilities seems to be the principal driver (Odum, 1971; Peyre et al., 2001; Crain et al., 2004; Silvestri et al., 2005; Touchette, 2006; Greenwood and MacFarlane, 2008). This zonation model predicts a tradeoff between competitive abilities and stress tolerance. Therefore, in an estuary the relative importance of the environment is expected to be bigger near the sandbar, where the ocean saltwater input creates an inhospitable environment for most species. Tidal influences decrease, and the environment becomes less limiting while heading up the estuary. With more species being physiologically able to inhabit the area, the importance of the biotic interactions increases. Thus, in estuaries, plant zonation is mainly controlled by abiotic drives in their lower limit (higher tidal influence) and by biotic drives in their upper limits (lower tidal influences) (Ungar, 1998; Castillo et al., 2000).

However, there are alternative models. It has been proposed that the competition would be more intense in harsh environments. The idea behind this model is that a smaller amount of resources would intensify the competitive process (Wiens 1977, Sherwood and Risser 1979). Another model predicts that the competition importance is the same, regardless of the environmental conditions. According to this model, the competitive process is equally important through all gradient, and what changes is the outcome species (Newman 1973, Tilman 1982, 1988).

Most studies regarding the relation between abiotic gradients and biotic interactions in tidal environmental were conducted in regular estuaries in medium and high latitudes of Northern Hemisphere (Costa et al., 2003). In the tropics, the relative importance of the rain is higher, and changes in the salinity conditions are expected to be more abrupt in space and time. Furthermore, in irregular estuaries there is a limited tidal effect, and so, the relative importance of the rain is even higher. In these environments, the salinity and frequencies and duration of the flooding cycles are unpredictable (Costa et al., 2003).

In regular estuaries, there is usually a clear and predictable pattern in plant distribution, and the species occur in relatively thin zones, with little niche overlapping (Vince and Allison, 1984; Pennings and Callaway, 1992). In irregular estuaries, the unpredictability of the flooding cycles and salinity conditions promote plant zonation of large zones and great niche overlapping (Baldwin and Mendelssohn, 1998). Therefore, it is not clear to which extent the current models can be used to make predictions regarding tropical estuaries (Costa et al., 2003), particularly the irregular ones, and plant zonation along tidal gradient in estuaries is one of the biggest gaps in our knowledge about costal environments (Crain et al., 2004).

We performed this work in a tropical irregular estuary, and our objective was to explain how the relative importance of the environmental and the biotic interactions change along the saline gradient. We predict that the combined action of the smaller tidal influence, higher pluviosity, and environmental unpredictability would lead this irregular estuary to have plant zonation patterns with large zones of occurrences, occasionally through the entire gradient, and a large niche overlapping. Therefore, that pattern would not be explainable through current tradeoff model.

2. Materials and methods

2.1 Study site

The Massaguaçu River Estuary (23°37'20''S e 54°21'25''O) is an irregular estuary, with a sandbar that breaches several times *per* year. The frequency of the breaching cycles ranges from few a days to more than one month. The time that the sandbar remains opened also varies, from one tidal cycle to more than 15 days. There are five main macrophytes banks within the estuary (banks A, B, C, D and E). Bank B is an island, and the others are linked to the estuary margin (fig. 1 – veja figura 1, pagina 13). The estuary is located in a region with humid tropical climate (*af*), with mild winter, rain in all months and with no biological dry season (Köeppen 1940).

Although the estuary's left margin is now anthropomorphized, it still presents riparian vegetation in almost all its extension. The right margin is better preserved, exhibiting Atlantic rain forest and several elements of *restinga* forest. The banks inside the estuary present dense formations of both aquatic and amphibians plants. To the best of our knowledge, there are neither studies regarding the estuary's floristic nor its conservational state, but also no history of direct disturbance in the last 30 years. The sandbar breaching is a natural event, but the artificial breaching is becoming more often, and the effects of this practice on the estuary flora are unknown.

2.2 Edaphic and floristic characterization

Over an aerial image we randomly chose 16 plots (5x5m) on each bank (total of 80 plots) and uploaded the plots location into a GPS device for field localization. In field we registered each species cover (m²) in each plot, collected a soil sample (and determined the edaphic characteristic), and measured the relative plot high. To measure the estuary water level, we installed a graduated scale in the estuary, where the zero represents the lowest level that the estuary water can reach (which occurs in the low tide when the sandbar is opened). Between June 2007 and June 2009 we made daily readings of the water level. The lower the level of the estuary, the faster it

rises. To linearise the data we created flooding classes (table 1), and classified the plots according to their relative high (veja table 1, pagina 88.).

2.3 Data analysis

For the floristic analysis we selected the most abundant species through a graph of species x abundances (“Whitaker plots”). With a presence/absence matrix we calculated the co-occurrence degree of the main species in each bank using the EcoSim 7.72 package (Gotelli and Entsminger, 2001) with settings at C-score index, with 10.000 permutations. In the software R (R Development Core R Development Core Team, 2006) we performed the variation partition analysis (Latiberté et al., 2009) to determine the relative importance of the environment and the space in the plant zonation.

3. Results

3.1 Estuary characterization

The estuary presented a longitudinal saline gradient. The salinity was three times higher on bank A (near the sandbar) when compared to bank E (Table 2). The distance to the sandbar is not the only driver of salinity. The relative high also plays an important role, and lower plots away from the sandbar can present a higher salinity than a higher plot near the bar. Therefore, the salinity values presented a high standard deviation, particularly in bank A, which has plots in a great number of heights. Although there is a slight reduction in the banks deep upstream (therefore, more plots in the higher flooding classes), all the banks have almost all the flooding classes. In other words, the vertical flooding gradient is relatively the same along the entire saline gradient.

Table 2. Average salinity on the Macrophyte banks in the Massaguaçu River Estuary.

Bank	Salinity (dsm ⁻¹)
A	0.93±0.65
B	1.02±0.46
C	0.60±0.34
D	0.52±0.44
E	0.36±0.24

3.2 Main species

We found 51 species of aquatic or amphibian plants in the Massaguaçu River Estuary, and classified 12 of them as abundant. Most species presented a relatively clear relation with the salinity. While *Crinum americanum* L., *Bacopa monnieri* (L.) Pennell, and *Eleocharis flavescens* (Poir.) Urb. were more abundant in the more saline portions, *Eleocharis interstincta* (Vahl) Roem. & Schul, *Sleria mitis* P.J. Bergius, *Rhynchospora corymbosa* (L.) Britton presented their higher densities away from the salt. *Typha domingensis* Pers. occurred only in the estuary's extremity, in the less saline part of the bank E. *Acrostichum danaeifolium* Langsd & Fisch and *Brachiaria mutica* (Forssk.) Stapf were denser in intermediary saline conditions. *Acroceras zizanioides* (Kunth) Dandy and *Echinochloa polystachya* (Kunth) Roberty, *Paspalum* sp. and did not present a clear zonation pattern along the saline gradient (table 2). The species also presented a clear relation with the flooding conditions. However, in this case, most species showed their higher density in a relative small number of intermediary flooding classes. Eight out of twelve species present their higher density between classes C50 and C80 (table 3).

3.3 Co-occurrence

Co-occurrence between most abundant species was smaller than expected by chance in the estuary salinity extremes: bank A (higher salinity) and D and E banks (lower salinity). On the other hand, bank C, that had presented intermediary salinity, presented a co-occurrence level bigger than the one expected by chance (table 4)

Table 3. Estuary main species, their favorite flooding class (FC) and total covering area (m²) in each machophyte bank.

Specie	Family	FC	A	B	C	D	E
<i>Crinum americanum</i> L.	Amarylidaceae	C70	163.34	124.57	122.30	125.11	60.63
<i>Eleocharis interstincta</i> (Vahl) Roem. & Schul	Cyperaceae	C60	37.39	0.00	54.65	95.08	107.81
<i>Bacopa monnieri</i> (L.) Pennell	Plantaginaceae	C80	93.26	71.98	37.51	14.43	0.00
<i>Acroceras zizanioides</i> (Kunth) Dandy	Poaceae	C50	39.19	0.00	40.21	47.85	58.36
<i>Eleocharis flavescens</i> (Poir.) Urb.	Cyperaceae	C70	83.41	22.48	13.42	4.12	0.00
<i>Rhynchospora corymbosa</i> (L.) Britton	Cyperaceae	C30	31.72	0.00	8.14	2.51	62.64
<i>Acrostichum danaeifolium</i> Langsd & Fisch	Pteridaceae	C70	6.20	24.30	30.93	0.00	0.20
<i>Typha domingensis</i> Pers.	Typhaceae	C40	0.00	0.00	0.00	0.00	53.62
<i>Paspalum</i> sp.	Poaceae	C30	33.00	0.00	0.00	1.65	7.21
<i>Echinochloa polystachya</i> (Kunth) Roberty	Poaceae	C60	0.00	8.77	1.03	25.96	2.83
<i>Brachiaria mutica</i> (Forssk.) Stapf	Poaceae	C70	0.00	1.09	4.12	31.76	0.00
<i>Sleria mitis</i> P.J. Bergius	Cyperaceae	C30	4.78	0.00	4.12	12.37	8.66

Table 4. Co-occurrence among the estuary most abundant species. This analysis measures the number of times (expressed herein %) the observed data presents a higher (% observed > expected) or a lower (% observed < expected) number of chessboard pairs when compared to the simulated data. The higher the number of chessboard pairs in the observed data (i. e. the higher the % observed > expected value), the smaller is the co-occurrence. A, B, C, D and E are the macrophyte banks.

	A	B	C	D	E
% observed > expected	0.999	0.275	0.025	0.984	0.906
% observed < expected	0.001	0.725	0.975	0.016	0.094

3.4 Variation partition

The higher the bank salinity, the higher is the environmental importance to plant zonation. Thus, the relative importance of the environment is higher in bank A, and almost null in bank E (table 5). The space importance does not seem to follow a pattern along the estuarine gradient.

Table 5. Environment and space importance on the plant zonation in the Massaguaçu River estuary.

A, B, C, D and E are the macrophyte banks.

	A	B	C	D	E
Environment (R ² ajusted)	0.43	0.34	0.17	0.20	0.01
Space (R ² ajusted)	0.17	0.01	0.17	0.31	0.12

4. Discussion

Salinity is the estuary's main limiting driver (Crain et al., 2004). The higher salt concentration near the sandbar has two main effects on the estuary plant zonation. The first one is that the salt seems to physiologically restrain the occurrence of several species, and appear to bring competitive advantages to a few number of halophytes plants (Castillo et al., 2000; Touchette, 2006). This leads the environment in the saline zone to have a bigger influence on the plant community. The second one is that, with a smaller number of species, the saltier zones tend to present no co-occurrence zonation patterns. At the other extremity, where the salinity is almost null, a great number of species is physiologically able to occur. With no salinity restraint, the environmental importance is reduced. On the bank E, where we found the smallest salinity values, the environmental importance for the plant community composition is reduced. With more individuals from more species able to inhabit a limited space, the competitive process gains importance. Therefore, the competitive exclusion of the halophyte species leads the low salinity zones to have smaller co-occurrence patterns as well. In the intermediaries zones, where the salinity is high enough to bring some competitive advantages to the halophyte species, but not high enough to restrain physiologically the non halophyte ones, there is a balance between environmental stress tolerance and competitive abilities (see Pennings and Callaway, 1992). The bigger number of species occurring in the same zone leads the average salinity zone to have great co-occurrence values (Fig. 2).

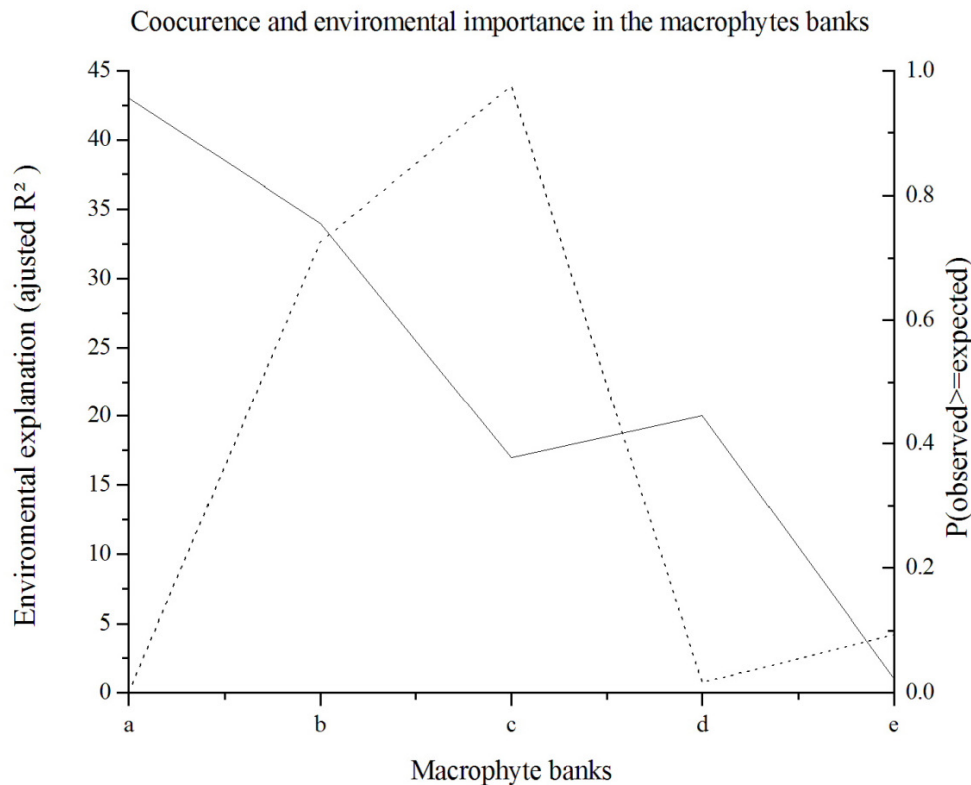


Figure 2. Co-occurrence (dotted line) and the environmental importance for plant zonation (continuous line) in the macrophyte bank in the Massaguaçu river estuary.

Changes in the plant composition along a saline gradient reflect both direct and indirect influence of the salt on each species. Therefore, looking at the species, and the way they interact may help understand these changes (Álvarez-Rogel et al., 2006). Most species in the Massaguaçu River Estuary presented clear distribution patterns along the saline gradient. *Bacopa monieri* and *Eleocharis flavescens*, for example, are two of the most abundant species in the bank A, and became rarer towards the estuary upstream. They are absent on the bank E. Nevertheless, they are widely spread in non saline environments, and the use of these species for decoration in fresh water tank is well documented. We also performed some tests in our laboratory, and we were able to grow both species in completely salt-free conditions. This suggests that salt brings competitive and not physiological advantages, and therefore its absence in the bank E does not result from the small amount of salt *per se*, but from the competitive outcome that they suffer. Otherwise, *Typha*

domingensis occurs only near the estuary's upper extremity (on the less saline zone of the bank E), but were present high densities. *T. domingensis* is commonly found in several aquatic environments, where densities are usually high. Thus, the lack of this species in the more saline zones is probably due to its salt intolerance (Glenn et al., 1995). In between, *C. americanum* is the most abundant specie on bank A, and its density diminishes with the salinity. This reduction seems to be accompanied by the increase of *Rhynchospora corymbosa*, *Eleocharis interstincta* and *Scleria mitis* densities, which appear in occasional spots on bank A, and become more abundant in non saline zones (Ribeiro et al, in press).

Plant zonation in regular estuaries is usually distributed clearly, with species occupying relatively thin zones along the gradients. The number and size of these zones vary among estuaries, but only few species may occur in several zones (Pielou and Routledge, 1976; Vince and Allison, 1984; King et al., 1990). The few studies regarding plant zonation in irregular tropical estuaries suggest a zonation with larger occurrence zones and niche overlapping (Costa et al., 2003). In The Massaguaçu River Estuary many species presented large occurrence zones. Eleven out of twelve species occurred in at least three banks, and seven are present in both extremities. This zonation pattern is consistent with what was proposed for irregular estuaries. In most irregular estuaries, the bar breaching is related to the rainy season. Although not as regular as the tidal cycles in regular estuaries, the rainy season breaches are relatively predictable. As the Massaguaçu River Estuary breaches several times *per* year, at completely irregular intervals, it presents a highly unpredictable tidal influence, which increases the spatial and temporal environmental diversity. The wide occurrence zone in the Massaguaçu River Estuary is probably related to its highly unpredictable environment. The unpredictability is a severe stress to most plants (Otte, 2001), and tends to prevent the competitive balance to be reached, which leads to a sub utilization of resources and so, a great niche overlapping (Russell et al., 1985). Furthermore, on a bigger time scale, the environmental stress can lead to an increase in the genetic diversity, and thus, the ecological niche (Pielou and Routledge, 1976).

The large occurrence zones suggest that, for most plants, the estuary abiotic conditions are not a limiting factor, and the environment acts as a regulator in the competitive interactions. Therefore, it would be expected that the importance of the environment to plant zonation in an irregular estuary would be relatively the same, regardless the condition. Nevertheless, that was not what we observed in the Massaguaçu River Estuary. As it happens in regular estuaries, the environmental importance is directly related to the tidal influence. Although the environmental unpredictability allows the species to occupy large zones along the estuary, these occurrences are usually occasional spots, and the main portions of the populations are concentrated in a much thinner zone. Therefore, we concluded that the plant zonation in the Massaguaçu River estuary corroborates the tradeoff model that was proposed for the regular estuaries in the Northern Hemisphere.

5. Conservation

The artificial sandbar breaching is a common practice in irregular estuaries and coastal lagoon in the Brazilian littoral (Suzuki et al., 2002; Santos et al., 2006; Branco et al., 2007). The breaching is frequently performed by the population, without the knowledge of any public department (Santos and Esteves, 2004). In the Massaguaçu River Estuary the artificial breaching is performed several times every year, frequently by the City Hall, to avoid flooding of the nearby road and houses. To the best of our knowledge, there are no studies regarding the impact of the breaching cycles on the estuary community, and the breaching seems to be conducted without any theoretical support. The close relation between the breaching cycle (and therefore, the tidal influence) and the plant zonation of the estuary suggests that the inadequate water level management jeopardizes not only the plant zonation, but all estuarine community (Hacker and Gainers, 1997). Understanding how this system works, and linking knowledge to its management are crucial for its conservation.

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CAPÍTULO 3

Functional Diversity along the Environmental Gradients in a Tropical Irregular Estuary⁵

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Abstract

Estuaries present two major environmental gradients: one vertical, related to flooding cycles and one horizontal, related to salinity. They are vastly accepted as most important abiotic drivers for plant zonation in estuaries. Most plants are adversely affected by salinity, and visible injuries are usually prelude of plant mortality. Thus, function changes in a saline gradient are expected to arise mainly from changes in species composition. To cope with flooding stress, several plants are able to develop morphologic modifications, and function changes in a flooding gradient can arise from changes in species composition or changes in individuals within a species. The role of each species in the community may vary drastically, and as traditional measures of diversity make an assumption that all species are equally different, they usually fail to predict community structure and function. Our objective in this work is to determine how functional diversity changes along the environmental gradients in a tropical irregular estuary, and which are the main abiotic drivers affecting these changes. We determined traits of all species and abiotic characteristics of 80 plots (25 m²) we randomly sampled in Massaguaçu River Estuary. We calculated richness and functional diversity of all plots, and through model selection related these indexes to the

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environment. Species richness was negatively related to flooding time, soil salinity, and fertility. Functional diversity was negatively related mainly to flooding time, suggesting that community is functionally resistant to other abiotic drivers, including salinity that is considered one of the main drivers in estuary plant zonation.

Keywords: flooding, plant zonation, richness, salinity, stress, tide.

1. Introduction

Estuaries present two major environmental gradients: one vertical, related to flooding cycles (Castillo et al., 2000; Pennings et al., 2005) and one horizontal, related to salinity (Silvestri et al., 2005; Greenwood & MacFarlane, 2008). In regular estuaries, where the connection with the ocean is permanent, there is a continued tidal influence, and both salinity and flooding gradient are relatively clear and predictable. In irregular ones, the connection with the ocean is sealed by a sandbar, and tidal influence is limited (Wolanski, 2007). In these cases, salinity gradient is less predictable in space and time (Costa et al., 2003), and tends to lose its importance as the freshwater inflow reduces its concentration. In the other hand, water level in an irregular estuary can become strictly higher than the high tide level (which is around the maximum level for a regular estuary), and thus, vertical gradient in an irregular estuary is expected to be much wider.

In regular estuaries, it is generally accepted that plant zonation follows a trade-off model in which there is an inverse relation between tolerance toward environmental stress and the competitive abilities (Costa et al., 2003; Pennings et al., 2005). According to this model, competitive dominant species would occupy the benign habitats and displace subordinate ones to harsh habitats (Crain et al., 2004). This results in a mainly qualitative changes in plant assemblages along the gradient, with most species presenting a relative thin occurrence zones (Vince & Allison,

1984; Pennings & Callaway, 1992). In irregular estuaries, environmental unpredictability promotes a wider plant zonation (Russell et al., 1985; Baldwin & Mendelssohn, 1998). There are evidences, though, that this wider zones are reflect of occasional spots, and most population are concentrated in a much thinner zone . Thus, changes in plant assemblages in irregular estuaries gradients can be more quantitative than qualitative. While the zonation patterns along estuaries gradients requires further investigation (Crain et al., 2004), the changes in these systems function along the gradient remain unknown.

Non halophyte species are adversely affected by salinity, and visible injuries are usually prelude of plant mortality (Kozlowski, 1997). Therefore, function changes in a saline gradient are expected to arise mainly from changes in specie composition. In the other hand, to cope with flooding stress, several plants are able to develop morphologic modifications, such as etiolation, development of aerenchyma tissue and adventitious roots (Kozlowski, 1997; Colmer & Flowers, 2008). These modifications allow amphibians plants to live with sporadic flooding. Thus, the vertical gradient can promote changes in system function by both changes in species composition and relative abundance or changes in individuals within a species.

The role of each species in the community may vary drastically. As traditional measures of diversity make an assumption that all species are equally different (Petchey et al., 2004), they usually fail to predict community structure and function (Díaz & Cabido, 2001; Ricotta, 2005). For example, when a group of species is replaced by other along the estuarine gradient, as long as both groups have about the same number of species and relative abundance, traditional measures of diversity are unable to detected differences, no matter how different these groups might be. Therefore, diversity measures that incorporate individual species characteristics in its values, such as functional diversity (FD), are gaining importance (Petchey & Gaston, 2006; Cianciaruso et al., 2009). FD is a trait-based approach (Violle et al., 2007) in which the diversity values arise from the functional diversity of characteristics of organisms (Cianciaruso et al., 2009).

Our objective in this work is to determine how FD changes along the environmental gradients in a tropical irregular estuary, and to assess the relative importance of the main abiotic drivers affecting these changes. We expect a higher FD variation between the extremes of the wide vertical gradient, with lower values in the deeper areas, where only a few number of species are able to cope with prolonged flooding, and higher values in less flooded areas, where there is a co-occurrence of great variety of plant forms. In other hand, we predict low variation in the FD values along the salinity gradient, as plants seems to be replaced by others of similar structure. Secondarily, we also aimed to determine how specie richness changes along the gradients, as so to have a traditional diversity index reference value.

2. Material and Methods

Study site

The Massaguaçu River estuary (23°37'20''S e 54°21'25''O) is an irregular estuary. The sandbar breaches several times *per* year, with cycles ranging from few days to more than one month. Duration of connection with the ocean also varies, from one tide change to more than 15 days. Breaching cycles are natural events, but a man-make breach in order to manage water level is a growing practice. The estuary is located in a region with humid tropical clime (*af*), with mild winter, rain in all months and with no biological dry season (Köeppen 1940). The estuary right margin is composed by Atlantic Rain Forest, in several conservational stages, also presenting elements from *restinga* vegetation. The left margin is an urbanized sand peninsula, which still presents, though, most of its riparian vegetation (figure 1 – veja figura na pagina 13). The estuary presents five major macrophytes banks, with formation of both aquatic and amphibian plants, including also some tree species.

Data collection

The estuary presents five major macrophytes banks. Using an aerial image, we random selected 16 plots (total of 80 plots) in each bank (5x5m - 25m²) in the estuary banks. We transferred the plot locations to a GPS device for field localization. In each plot we measured the height and collected a leaf of six individuals chosen by chance of each species. We photographed the leaves, and through an image software, measured the foliar area and petiole size. After that, we dried the leaves (60°C, till mass stabilization) and weight them. This allowed us to calculate the specific foliar area. We classified the species based on their life and growth form (modified from Cornelissen et al., 2003). We also qualified species regarding the presence/absence of lenticels and specific adaptation to flotation (table 1). We collected soil samples (0-15cm), and sent to analysis of main nutrients, organic matter, pH and electric conductivity (hereafter, salinity) (Camargo et al., 2009).

We installed a graduated scale in the estuary, where the zero represents the lowest level that the estuary water can reach (during low tide, with the sandbar opened). From June 2007 to June 2009 we made daily reading of the water level, and we also measured the relative height of each plot. Based on the flooding time, we created flooding classes (see Ribeiro et al., 2011), and, according to its relative height, classified each plot into these classes.

Based on a correlation analysis (Pearson) we removed correlated explanatory variables, and then calculated the FD value (Petchey & Gaston, 2002; Petchey & Gaston, 2006) of the estuary plots using average trait values *per species per plot* (spFD, see Cianciaruso et al., 2009). We performed the analyses in a R environment (R Development Core Team, 2008), using the *gower* distance. After that, we related the FD values with environmental variable through a model selection by Akaike criterion (Burnham & Anderson, 2002), using SAM (Rangel et al., 2009). We also related Richness and environmental variable, as so to have a traditional diversity index

reference value. We did not use diversity because species abundances were not in the same unit (macrophytes were in m² and trees in units).

Table 1. Traits used to measure the functional diversity.

Trait	Possible responses	Description	Reference
Height	Linear measure	Live plant height	(Cornelissen et al., 2003)
Specific foliar area	Quadratic measure	Foliar area/leaf dry weight	(Cornelissen et al., 2003)
Petiole	Linear measure	Size of the leaf petiole.	
Flotation	Yes/No	Presence of specific adaptations to floating (note the floatability itself)	
Lenticels	Yes/No	Presence of lenticels.	
Life form	A	Fixed in the substrate, shoot and gems partially submerged	(modified from Cornelissen et al., 2003)
	B	Fixed in the substrate, shoot partially submerged, gems completely submerged	
	C	Fixed in the substrate, shoot and gems completely submerged	
	D	Fixed in the substrate, floating leave.	
	Phanerogames Chamephytes G	Amphibius phanerogames Amphibius chamephytes Epiphytes	
Growth form	Tree	Tree	(modified from Cornelissen et al., 2003)
	Submersed plant	Submersed plant, exclude touceiras	
	Submersed touceiras	Submersed touceiras	
	Floating	All leave floating on water.	
	Leaner	Fixed in the substrate, with shoots leaning on water. Plant is able to float, though show no specific adaptation for that. Bottom leaves are submererged.	
	Epiphytes	Epiphytes	
	Flooded plan	Grow perpendicular to water column, and became submerged as the water level rises.	
	Amphibius basil	Small plant (less that 30 cm), resistant to occasional flooding.	

3. Results

In Massaguaçu River Estuary, plots richness ranged from one to 11, with average of 3.67. Richer plots are usually located in higher (therefore, less flooded) region in the estuary and presented a combination of macrophytes, trees and lianes. In saline gradient, richer plots are related to non-saline regions, although low-rich plots occur all along the gradient. The average model according to AICc related richness mainly to Flooding Time (Flt), calcium and salinity (Table 2).

Lower plots are occupied by few species able to cope with prolonged submerged times. This species usually share most of their functional characteristics (eg. Life and Growth form), and therefore, lower plots generally presented low FD values. A strictly great number of species seems to be able to live in sporadic-flooding condition. Higher plots presented groups of plants with a wide range of functional traits (from 5cm macrophytes to 5m trees, from grass to pteridophyte lianes). Higher plots usually associated to higher FD values, which leaded to a marked variation of community FD along flooding gradient. The average model pointed out Flt as, by far, the most important variable to explain changes in FD values in the estuary (Table 3).

Table 2 – Averaged models, using Akaike Weights (AICc w_i) to explain chances in species richness in the Massaguaçu River Estuary.

Variable	Importance	Coeff	Std Coeff	Std Error	t	95% Low	95% Up
Constant	-	8.688	0	1.249	6.955	6.24	11.136
Organic matter	0.242	-0.002	-0.022	0.003	-0.8	-0.008	0.003
Ph	0.261	-0.106	-0.032	0.106	-1.002	-0.314	0.102
P	0.238	0.003	0.01	0.007	0.347	-0.012	0.017
K	0.452	-0.296	-0.161	0.101	-2.925	-0.494	-0.098
Salinity	0.474	-0.595	-0.17	0.201	-2.957	-0.989	-0.201
Calcium	0.509	-0.018	-0.161	0.006	-2.984	-0.03	-0.006
Flooding Time	0.999	-0.059	-0.481	0.014	-4.327	-0.086	-0.032
n: 71	r: 0.59	r²: 0.349	r² Adj: 0.299	AICc: 268.845			

Table 3 – Averaged models, using Akaike Weights (AICc wi) to explain changes in species Functional Diversity in the Massaguaçu River Estuary.

Variable	Importance	Coeff	Std Coeff	Std Error	t	95% Low	95% Up
Constant	-	1.762	0	0.352	5.012	1.073	2.451
Organic matter	0.236	<.001	0.003	<.001	0.104	-0.001	0.001
Ph	0.328	0.084	0.105	0.031	2.709	0.023	0.144
P	0.237	<.001	0.002	0.002	0.061	-0.003	0.004
K	0.252	0.019	0.044	0.014	1.416	-0.007	0.046
Salinity	0.246	-0.028	-0.033	0.026	-1.092	-0.078	0.022
Calcium	1	-0.015	-0.523	0.003	-4.791	-0.022	-0.009
Flooding Time	0.416	-0.004	-0.14	0.001	-2.975	-0.006	-0.001
n: 71 r: 0.556 r²: 0.309 r² Adj: 0.256 AICc: 70.146							

4. Discussion

Changes in environmental conditions along gradients are generally followed by changes in species composition. In Massaguaçu River estuary, richness increases when Ftl, calcium and salinity decreases. Flooding and salinity are vastly escorted by literature as the main abiotic drivers for plant zonation in estuaries (Touchette, 2006; Greenwood & MacFarlane, 2008; Sharpe & Baldwin, 2009), and low values of richness in salty and/or flooded plots are expected. Relationships between calcium and richness in estuaries are less clear, and require further investigation. In the other hand, Ftl seems to be the only important variable to explain to FD values along the environmental gradient. This suggests that stress caused by salinity and calcium reflects in changes in the number of species but not in the community function.

In salinity gradient, changes in species zonation usually arise from modification in competitive patterns, with more competitive species replacing more tolerant ones as salinity decreases (Crain et al., 2004). However, competition frequently happens between species that are morphologic alike, and changes in species composition do not necessarily reflect changes in the community structure (Loiola et al., 2010). In Massaguaçu River Estuary, there is a marked

resemblance in several morphological characteristics among the different main species along the gradient (Ribeiro et al., 2011), suggesting that changes in species composition caused by different quantities of salt has small effects over community function. Furthermore, the unpredictability of irregular estuaries tends to prevent the competitive balance to be reached (Russell et al., 1985) and increase the importance of stochastic events in species zonation. Therefore, irregular estuaries plants usually present wide occurrence zones (Costa et al., 2003). With a great number of species occupying large horizontal zones in the estuary, it is expected a small variability in FD values along salinity gradient.

Changes along the flooding gradient affect community differently. First, because amphibians species can present morphological different depending upon they are flooded or not (Kozłowski, 1997). For example, In Massaguaçu River Estuary the height of some species seems to be sensitive to frequency and duration of the flooding. Besides, species such as *Bacopa monnieri* (L.) Pennell only flourishes while non-flooded. This might lead to changes in community structure without changing species composition. Second, because even terrestrial plants can live with sporadic low-duration flooding. In Massaguaçu River Estuary there are several species, such as *Rhynchospora sp*, *Scleria latifolia* Sw., and some *Eugene* species, that are characteristic of adjacent forest, but that are found in the sporadically flooded plots. Furthermore, several aquatic plants can live in non flooded environment, as long as they are not exposed to water shortage. Thus, higher plots can support the presence of plants with different flooding preferences. Third, as the soil of higher plots is usually exposed but gets flooded when estuary water level is high enough, it is likely to receive both floating seeds to during the flooding and seeds from the adjacent forest while exposed. This makes the higher plots much more likely to be colonized, by a great variety of species, and also increases the occurrence of occasional species. Colonization in low soil is much more unlikely to happen. As they are rarely exposed, seeds have few opportunities to reach the soil. Is this case, sexual reproduction is restricted to a few number of species, and vegetative reproduction is more important.

With differences in specific morphology, range of supported species, and colonization opportunities, lower and higher plots present different species composition and structure. Lower plots presents a relative small number of species, adapted to cope with frequent and long submerged periods. These species are, under several aspects, such as growth form and leaf structure, very similar to each other. Plots that are flooded sporadically, during short periods present a greater number of species, with a wide range of morphological characteristics: small herbaceous plants, grasses, trees, and epiphytes. According, lower plots are likely to present small FD values, and higher plots to present high FD values. This creates a marked gradient in FD values along the flooding gradient, and explain why flooding is the main driver in FD in the Massaguaçu River Estuary.

Contrary to what the trade-off model predicts, some species can be an aggressive competitor and at the same time, very tolerant to abiotic stress (Emery et al., 2001; Costa et al., 2003; Ribeiro et al., 2011). *Crinum americanum* L. is one of these species (see Ribeiro et al., 2011), and were present in about 70% of the sampled plots. With most plots sharing its presence, changes in richness and FD along the gradient are likely to be masked by the presence of this particular species.

In conclusion, we showed that species composition changes along salinity gradient, but Massaguaçu River Estuary flora is functionally resistant to these changes. Flt has a greater impact in plant community, and are related to reducing both richness and FD. There are very few studies regarding changes in FD in estuarine gradients, and the differences between richness and FD response towards environmental gradients support that a trait-based approach may be more helpful to understand estuarine community function.

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CAPÍTULO 4

Spatial distribution of *Crinum americanum* L. in tropical blind estuary: hydrologic, edaphic and biotic drivers.⁶

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ABSTRACT

The competitive abilities of a given species are inversely proportional to its tolerance to environmental stress. Thus, in estuaries, vegetation is generally controlled by salinity and flooding in their lower limits, and by biotic drivers in their upper limits. *Crinum americanum* L. is vastly distributed over flooded regions of American seacoast, frequently associated with stressful habitats. We aimed to explain the role of hydrologic, edaphic, and biotic drivers in the distribution of this species on the Massaguaçu River estuary, Southeastern Brazil (23°37'20"S and 54°21'25"W). We sampled randomly 400 plots in the estuary, and registered covering of all species, the height of the *C. americanum* individuals, and the relative height of the plots. We collected soil samples from every five plots. We measured the estuary level daily for two years. We used Correspondence Analysis, Simple and Canonical, and graphic analysis. The salinity has explained the major part of the observed pattern, and the *C. americanum* population was positively related to it. The estuary level was also important. *C. americanum* has presented higher densities in intermediary flooding classes than in the extremes of the gradient. Species reduction in regions of low salinity or its absence has probably been due to the highly competitive environment, and not to the lack of salt *per se*.

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1. Introduction

In estuaries, the distribution and abundance of species are directly related to their capacity of bearing environmental conditions and to their competitive abilities (Crain et al., 2004; Greenwood and MacFarlane, 2008). In these environments, the major determinant factors for the plant assemblage are salinity and flooding cycles (Bockelmann et al., 2002; Costa et al., 2003; Silvestri et al., 2005). Generally, species' competitive abilities are inversely proportional to their tolerance towards environmental stresses (Pennings et al., 2005). Thus, along with the salinity gradient of an estuary, the competitive dominant species would occupy the physically benign habitats and displace subordinate ones to physically harsh habitats (Crain et al., 2004). This way, species distribution in an estuary is usually controlled by salinity and exposure to flooding in its lower limits, and biologically controlled in its upper limits (Ungar, 1998; Castillo et al., 2000; Pennings et al., 2005).

Most experimental studies on species zonation, along with salt marshes environmental gradients, have been conducted in estuaries with permanent connection with the ocean, at middle and high latitudes of Northern Hemisphere (Costa et al., 2003). In tropical estuaries of the Southern Hemisphere, pluviosity has a relatively higher importance, and salinity gradients are expected to be more abrupt. In blind estuaries, where the connection with the ocean is sporadic (see Hume et al., 2007), the relative importance of the rain is even bigger, and both salinity and flooding cycles are less predictable. Thus, it is not clear to what extent the information about regular Northern salt marshes can be extrapolated to tropical blind estuaries (Costa et al., 2003). Plant zonation along with salinity gradients represent a major gap in the knowledge of tidal environments, and understanding this is crucial for both conservation and restoration of coastal marsh systems (Crain et al., 2004).

Crinum americanum L. (Amaryllidaceae) is widely distributed throughout flooded regions, swamps and rivers of the America seacoast, frequently associated with ecologically stressful areas (Meerow et al., 2003). This is a fast growing species, which is salt and flooding resistant, with large and salt-resistant floating seeds, and strong allelopathic potential (Ribeiro et al., 2009). *C. americanum* seems to be highly aggressive, occupying several large areas (Mayer et al., 1998).

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In a blind tropical estuary, with no biologically dry season, we noticed that although *C. americanum* is evident all along the estuary, it seems to be highly abundant in areas next to the sandbar. Its vertical zonation also seems to present a pattern, with lower densities in the superior and inferior extremes in the estuary. We expect the *C. americanum* distribution pattern to arise mainly from salinity in the horizontal gradient and mainly from the flooding exposure in the vertical gradient, and both gradients to be important to determine the interspecific interactions patterns. Thus, to test this hypothesis, our objective were twofold: to better characterize the distribution of *C. americanum* along the estuary and to determine how this distribution can be explained by (1) estuary edaphic characteristics, (2) flooding cycles and, (3) inter-specific interactions.

2. Materials and methods

Study site. The estuary of the Massaguaçu River (23° 37' 20" S and 54° 21' 25" W) is a blind estuary. The sandbar which separates it from the ocean opens a few times *per* year, and on these occasions, the level of the water may result in more than a 2-m decrease. The frequency and duration of these events are irregular, and expose the flora to sudden and unpredictable changes in the environmental conditions. Although the opening cycles of the bar are natural events, the opening by anthropic action has been on the increase. We accomplished this experiment in five large banks of macrophytes belonging to the estuary. Four of them are linked to the estuary margin, and one is an island. These banks are distributed longitudinally in the estuary, and offer a propitious condition for studies of zonation in environmental gradients (supplementary data 1).

Floristic. The use of cover values to quantify populations has been largely used for species when it is not possible to count individuals (Mueller-Dombois and Ellenberg, 1974). Generally, the density in which the species occurs is not taken into account, and same-sized areas with either sparse or dense emergencies get the same cover value. The method described as follows is an adaptation of the standard procedures to include the values of different densities into the cover value. To determine the distribution and abundance of species in the estuary, we sampled randomly 80 plots (5 × 5 m) on each bank (400 plots total), and transferred the coordinates of these plots to a GPS for future field localization. We registered the cover areas (m²) of the species which occurred in each one of the plots. We classified the densities of these areas into three categories: I – low (1–33% of the plot area covered by the species), II – medium (34–66%) and III – high (67–100%). As a species may occur in more than one spot within a single plot, and as these spots may have different densities, we calculated intermediate values for each density category (low – 16%, medium – 50% and high – 83%) and multiplied them by the cover area values from each one of these spots. By doing so, the cover value of each spot incorporated the density of the species occurring in it. The sum of the covers of each spot generated a single cover value per species per plot (supplementary data 2). To *C. americanum* the high, medium and low densities corresponded to 50, 30 and 10 individuals per m². Thus, depending on the analysis we could use the density (e.g. comparison with the cover area of other species) or the number of individuals (e.g. determination of the size of the population). In each plot we measured the height of six individuals of *C. americanum*, chosen at random. For the analysis, we used only the more abundant species, selected through the curve species-abundance (“Whittaker plots”).

Edaphic relationships. To determine the edaphic characteristics of the estuary, we collected soil samples for every five plots (16 per bank, 80 total) and determined the pH values, organic material, the micro and macro nutrient contents, sodium, electric conductivity,

Table 1

Flooding classes of the Massaguaçu river estuary, with the minimum and maximum depths (cm) and the flooding time (percent) of each class.

Flooding classes	Minimum depth	Maximum depth	Flooding time (%)
C100	–50	0	100.00
C90	1	40	89.97
C80	41	66	79.94
C70	67	90	68.71
C60	91	110	57.63
C50	111	120	47.31
C40	121	138	37.87
C30	139	151	26.65
C20	152	168	14.82
C10	169	220	6.29

and flooding. For the analyses, we created a salinity index, from the multiplication of the sodium and electric conductivity.

Hydrologic relationships. To determine the variation of the estuary level, from July 2007 to July 2009, we made daily readings of the relative level of the water (we established zero as the lowest level that the estuary reaches, which occurs in the low tide with the sand bar opened). We measured relative height of each plot as well. The lower the level of the estuary is, the faster it rises. Thus, the difference of the flooding time is smaller between the lowest plots, and bigger between the highest ones. To analyze the data more precisely in the biological sense, we grouped the levels of the estuary in flooding classes (Table 1).

Data analyses. We determined the relation between the density and height of the *C. americanum* population, and the estuary soil characteristics through Canonical Correspondence Analysis. We used the Monte Carlo with 1000 permutations to test its significance. We used Correspondence Analysis to relate the density with the flooding class. To compare the distribution of *C. americanum* along the estuary concerning the distribution of determined species, we calculated the occupation of each one of them in all banks, plotting its densities concerning the flooding classes. To perform a graphic analysis of the *C. americanum* distribution along the estuary, we made a contour map, using its densities as *z* values.

3. Results

3.1. Description of *C. americanum* distribution

C. americanum is the most abundant species of the estuary. Its density was higher nearby the bar, but it was present in all of its extension (supplementary data 3). This species presented high dominance in the more saline portion of the estuary, where on several occasions was the only species of the plot. By its density and cover, we estimated its population in around 3430 thousand individuals. In the Massaguaçu River estuary, the reproduction of *C. americanum* can happen sexually, through the production of a high number of seeds, and non sexually, through rhizomes. For this reason is not possible to know in the field if it is a genetic unit or a clone. Thus, we call individual any emergency. In bank D, and especially in bank E, where *C. americanum* occurred in lower densities, its population was estimated in more than 1.7 million individuals. The height of the individuals along the estuary did not vary much, and the total average was 1.07 m (Table 2).

3.2. Edaphic relationships

Salinity was the most important edaphic factor for the distribution and density of *C. americanum*, and the higher its values, the higher its densities. The other elements analyzed seemed to have little or no influence over the density of *C. americanum*. The analysis did not highlight any edaphic factor as determinant for the height

Table 2

Area (m²), number of individual, density (individual/m²) and average height of the *C. americanum* population in the macrophytes bank in the Massaguaçu river estuary.

	Area	Individuals	Density	Height
A	52434.97	985.643	18.8	1.05
B	20931.72	351.759	16.8	1.14
C	23759.31	354.042	14.9	1.06
D	95027.43	1086.816	11.4	1.03
E	86546.28	652.056	7.5	1.09
Total	278699.7	3430.316	13.9	1.07

of the individuals of this species in the Massaguaçu River estuary (supplementary data 4).

3.3. Exposure to flooding

The distribution and density of *C. americanum* in the Massaguaçu River estuary were significantly related to the exposure to flooding. Mean and high densities occurred preferably in the flooding classes C70 and C80. The lowest density occurred in the more flooded (C90) and less flooded (C60) classes. The absence of this species was related to the extreme class (C100 and C50 and lower class) (supplementary data 5).

3.4. Biotic relationships

The estuary had 51 species of aquatic or amphibian plants. We classified 12 species as abundant (Table 3). These species represented altogether near 93% of the total plant coverage of the estuary. *C. americanum* L., *Bacopa monnieri* (L.) Wettst., *Eleocharis flavescens* (Poir.) Urb., and *Acrostichum danaeifolium* Langsd. & Fisch. presented a preference for the more saline portion, being more abundant if closer to the bar. *Eleocharis interstincta* (Vahl) Roem. & Schult., *Typha domingensis* Pers., *Scleria mitis* P. J. Berge, and *Rhynchospora corymbosa* (L.) Britton were more abundant in the less saline ones. *Acroceras zizanioides* (HBK) Dandy, *Echinochloa polystachya* (Kunth) Hitchc, *Paspalum* sp. and *Brachiaria mutica*

Table 3

The principal species of Massaguaçu river estuary.

Species	Family
<i>Crinum americanum</i> L.	Amaryllidaceae
<i>Eleocharis interstincta</i> (Vahl) Roem. & Schul	Cyperaceae
<i>Bacopa monnieri</i> (L.) Wettst.	Plantaginaceae
<i>Acroceras zizanioides</i> (Kunth) Dandy	Poaceae
<i>Eleocharis flavescens</i> (Poir.) Urb.	Cyperaceae
<i>Rhynchospora corymbosa</i> (L.) Britton	Cyperaceae
<i>Acrostichum danaeifolium</i> Langsd & Fisch	Pteridaceae
<i>Typha domingensis</i> Pers.	Typhaceae
<i>Paspalum</i> sp.	Poaceae
<i>Echinochloa polystachya</i> (Kunth) Hitchc.	Poaceae
<i>Brachiaria mutica</i> (Forssk.) Stapf	Poaceae
<i>Scleria mitis</i> P.J. Bergius	Cyperaceae

(Forssk) Stapf did not present a clear distribution pattern along the saline gradient.

The relationship between richness and diversity, and the saline gradient was not clear, and extremity banks (A and E) presented similar values for these index. On the other hand, the reduction of the *C. americanum* population in the less saline portions was accompanied by an increase of density of determined species (Fig. 1). These species were morphologically similar to *C. americanum*, and occupied similar flooding classes. The density of the species per flooding class per bank showed the decline in the *C. americanum* population and the subsequent increase in the other ones (Fig. 2).

4. Discussion

Salinity and flooding are determinant factors to the zonation of *C. americanum* in the Massaguaçu River estuary. The density of this species follows the saline gradient of the estuary, being higher in the portions with more salt. The flooding restricts *C. americanum* to specific heights of the estuary, and this species is almost absent in the extreme flooding classes. As it is maintained in non flooding conditions as an ornamental plant, the absence of this species from lower flooding class might not be related to the lack of flooding

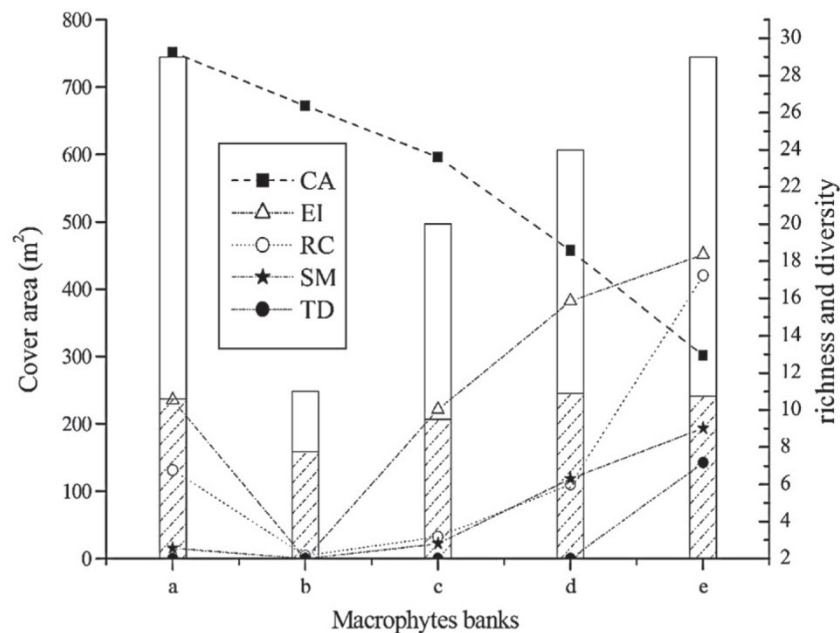


Fig. 1. Distribution (in m² in the 80 plots) of *Crinum americanum* (CA), *Eleocharis interstincta* (EI), *Rhynchospora corymbosa* (RC), *Scleria mitis* (SM) and *Typha domingensis* (TD) in the five macrophytes banks of the Massaguaçu River estuary. The full bar represents the richness and the bar with hashed lines represents the diversity (Shannon × 5).

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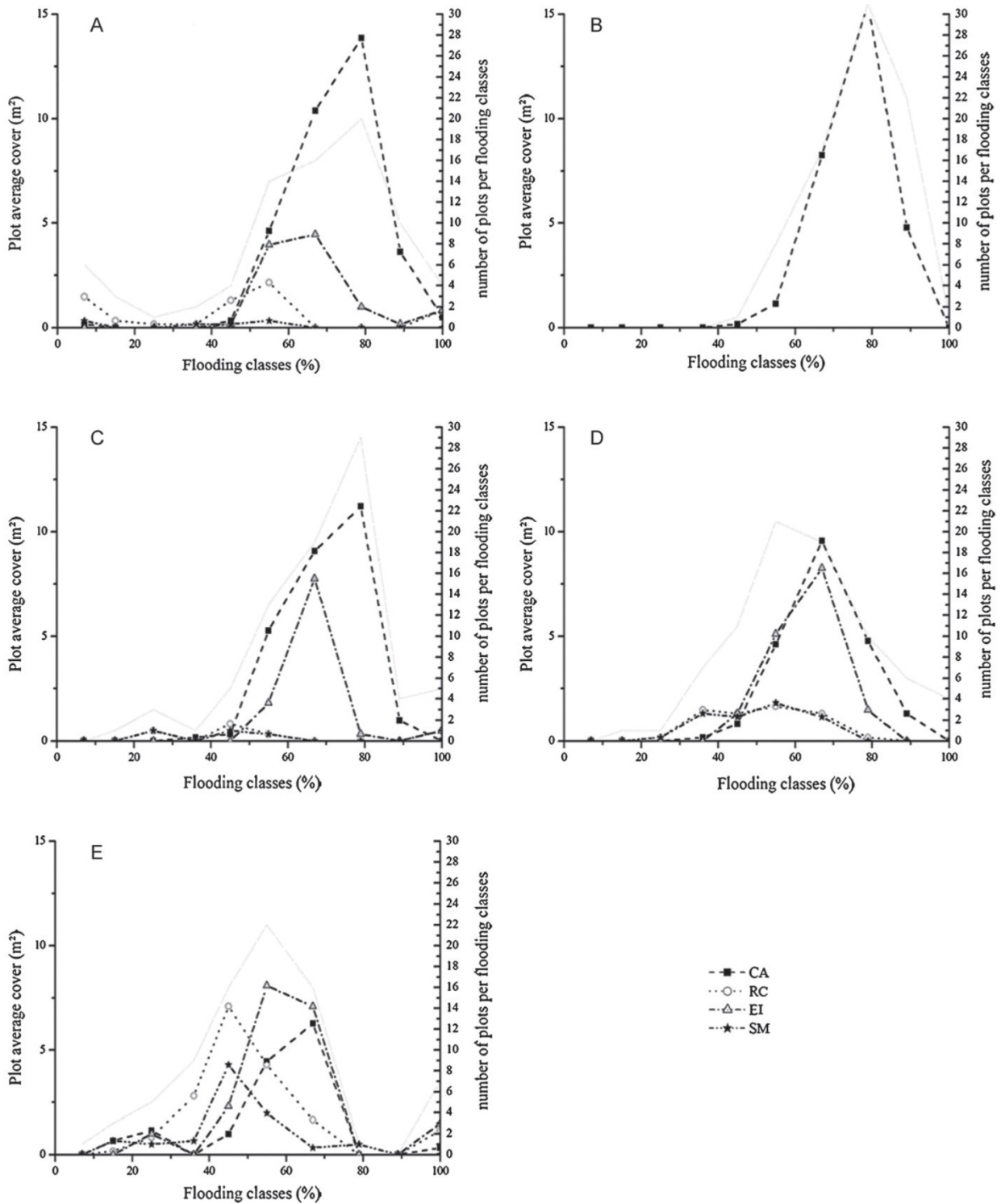


Fig. 2. Occupation of the flooding classes in each macrophytes banks (A, B, C, D and E). The line with symbols represents *Crinum americanum* (CA), *Eleocharis interstincta* (EI), *Rhynchospora corymbosa* (RC) and *Scleria mitis* (SM). The single line represents the number classes in each flooding classes.

itself. We believe that this occurs due to the arboreal component and its consequent shadowing, as this is the major limiting factor for aquatic plants (Phillips et al., 1978). However, to the best of our knowledge, no work has been done to determine the cause of this phenomenon. The absence in the very flooded class may be related to difficulties in colonization, since the floating seeds of *C. americanum* have less chances of getting fixed in a substratum which is exposed for less time. This lacks investigation as well.

There is little information on ecology of *C. americanum*, and most information that is available on its biology comes from its cultivation. It is a rustic species, tolerant to salinity and little demanding about the soil characteristics (Gilman, 1999; Ribeiro et al., 2009). In the Massaguaçu River estuary, pH, macro and micro nutrients have little influence over the distribution or size of *C. americanum*. As it happens with most estuarine plants, the main edaphic factor to the distribution of this species is the salinity (Touchette, 2006; Greenwood and MacFarlane, 2008).

It is unknown how the salt interferes physiologically in *C. americanum* development. It is unlikely that low quantities of salt should be a limiting factor, though. The high number of records of its cultivation in fresh water and the size of its population in banks D and E itself support this idea. Thus, the presence of salt would bring competitive advantages to the *C. americanum* (see Ungar, 1998). Several authors have demonstrated how variations in salinity influence the interspecific competition in a saline gradient (Peyre et al., 2001; Crain et al., 2004; Silvestri et al., 2005; Touchette, 2006; Greenwood and MacFarlane, 2008), and frequently most tolerances to environmental factors are related to smaller competitive abilities. In this context, the presence of salt provides competitive advantages to *C. americanum*, increasing its dominance in the saline portions. As salinity decreases, other species become more efficient and the competitive interactions reduce the density of *C. americanum*.

For some species this relation is quite clear. *E. interstincta*, *T. dominguisis*, *S. mitis* and *R. corymbosa* were more abundant in the less saline portions, and the increase of its populations was followed by the reduction of population of *C. americanum*. These species are structurally alike, and occupy similar flooding classes. This relation was best noticed in the distribution of bank E (Fig. 2E), where the population of *C. americanum* presented a valley in the flooding classes where *R. corymbosa* and *S. mitis* presented maximum densities. To other species this relation is not so clear. *B. monnieri*, *E. flavecens*, and *A. danaeifolium*, for instance, also prefer the more saline portions, and their distributions present patterns similar to *C. americanum*, suggesting that they respond in a similar fashion to changes in the environment. *A. zizanioides* and *E. polystachya* do not seem to follow a salinity pattern, and thus it is not possible to establish its role along the salinity gradient.

The reduction of *C. americanum* in the less saline portions would not be related to the changes in number or in the species composition, but with the increase of population of some species. In that sense, the higher diversity values in the less saline portions (especially D and E) would be consequence and not cause of the reduction of the population of *C. americanum*. The hypothesis that reduction of population of *C. americanum* could be related to the increase of population of determined species seems to be quite plausible. *C. americanum* is a predominantly coastal species (Meerow et al., 2003) and *E. interstincta*, *R. corymbosa*, *S. mitis* and *T. dominguisis* are widely distributed in flooding regions in general, often occurring in environments with no salinity (Pott and Pott, 2000).

Competition seems to influence the vertical occupation of the estuary as well. *C. americanum* is dominant in two flooding classes C70 and C80 (Supplementary data 4). Its density is smaller in the

portions where competition is higher, but it occupies more flooding classes, suggesting that the presence of other species detours this species from its optimum flooding classes.

Even in the less saline portions, where it appears as a subordinate form, *C. americanum* is still a highly representative species. This suggests that the trade of tolerance to stresses versus competitive abilities is not always true, and that one environmentally tolerant species may also be an efficient competitor (Emery et al., 2001; Costa et al., 2003).

Acknowledgments

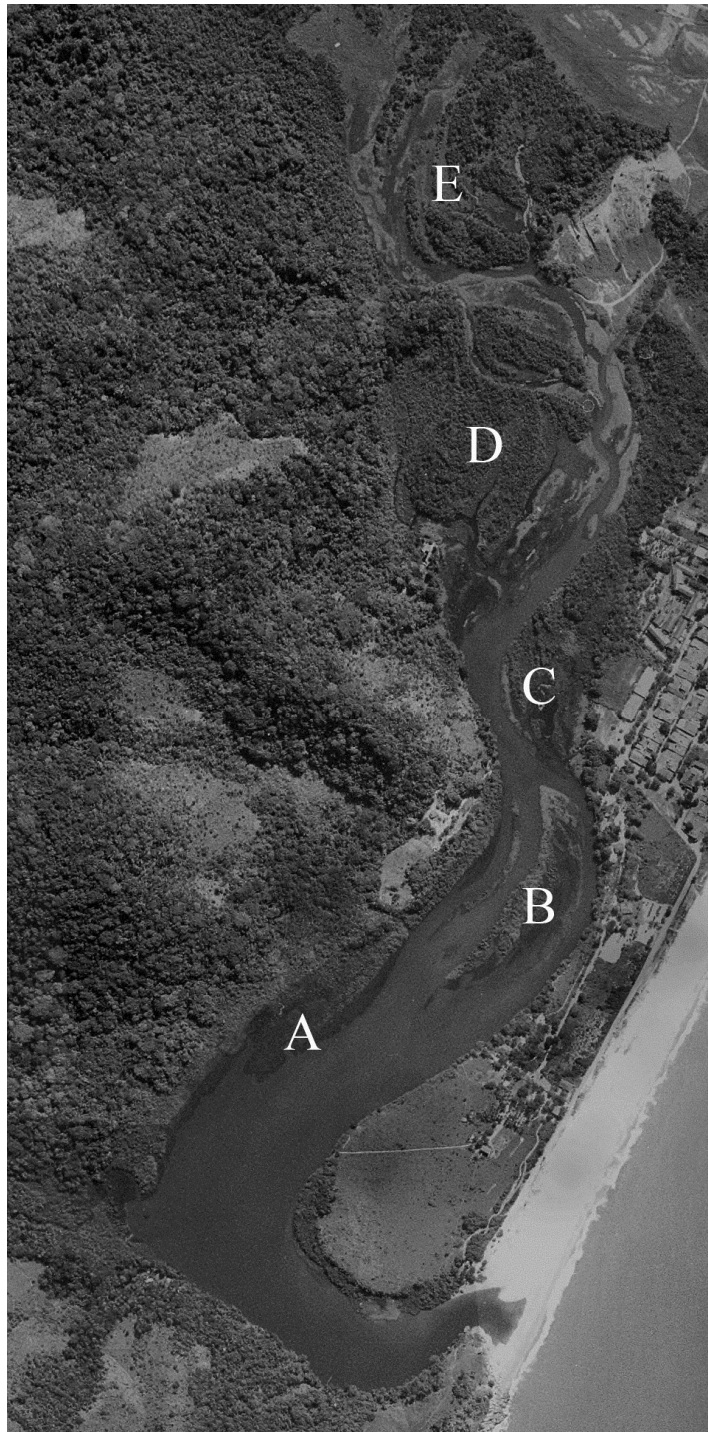
We would like to acknowledge the Conselho Nacional de Desenvolvimento Científico (CNPq) and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for funding this research. We also would like to thank Mateus Silveira for all the field support.

Appendix A. Supplementary data

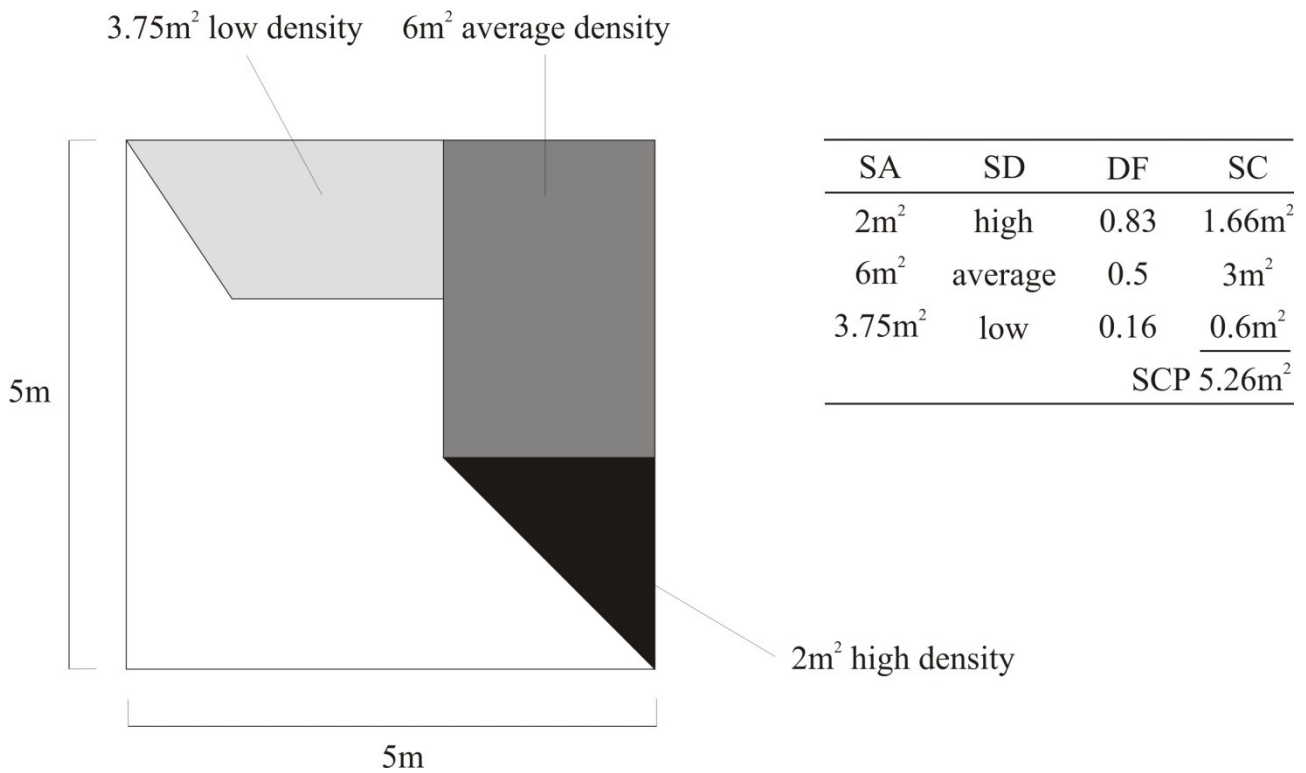
Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.envexpbot.2010.12.011.

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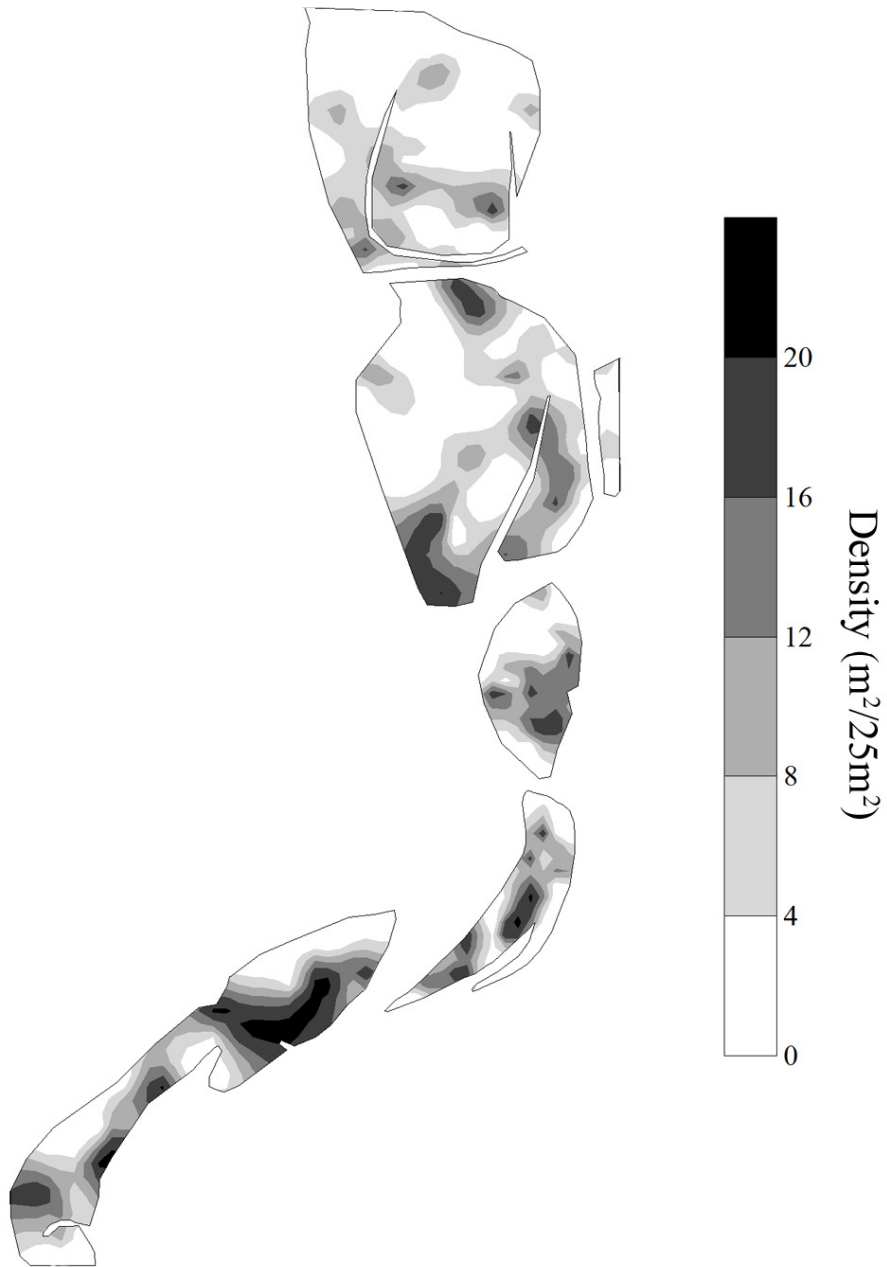
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Supplementary data 1. Massaguaçu River Estuary. The letter indicates the macrophyte banks. The bank B is an island, and the other are connected to the estuary margin.

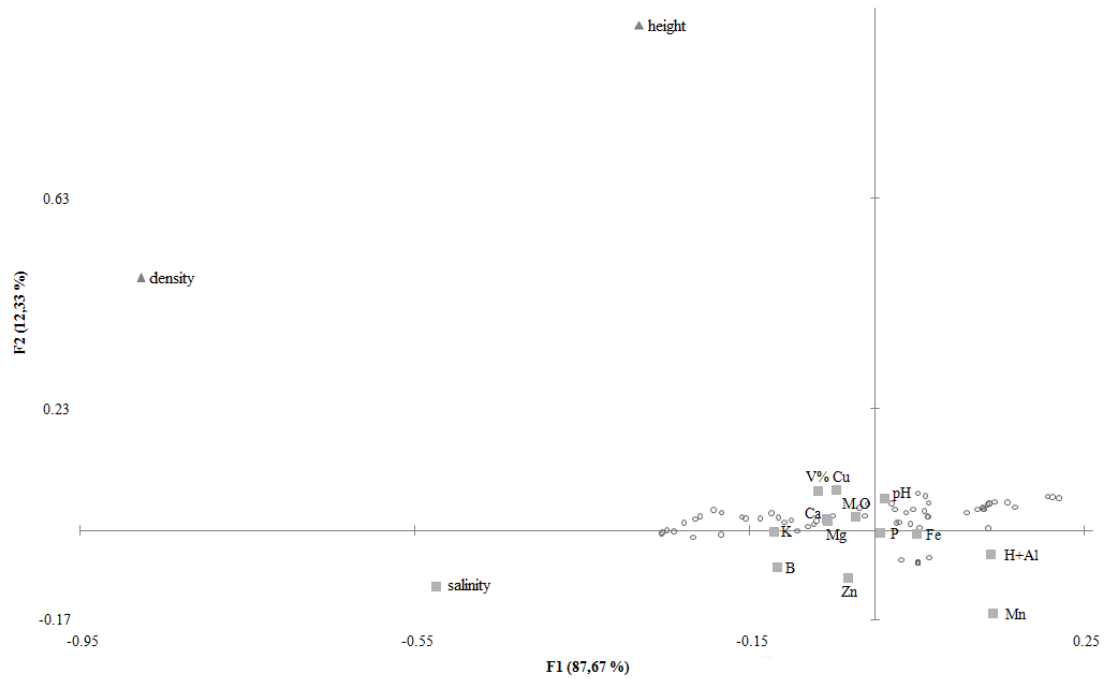


Supplementary data 2. Hypothetic 5x5m plot, with a species occurring in three spots of different density. A spot with 2m² where the species presents a high spot density (SD). Thus, multiplying the 2m² spot area (SA) by the 0.83 spot density factor (DF) with arise in a spot cover (SC) of 1.66 m². Another spot with 6 m² and average density, producing a 3 m² spot cover and a spot with 3.75 m² at low density, with a spot cover value equal to 0.6 m². Summing the three SC (2, 1.66 and 0.6 m²) with arise at one unique species cover in the plot (SCP) of 5.26 m².



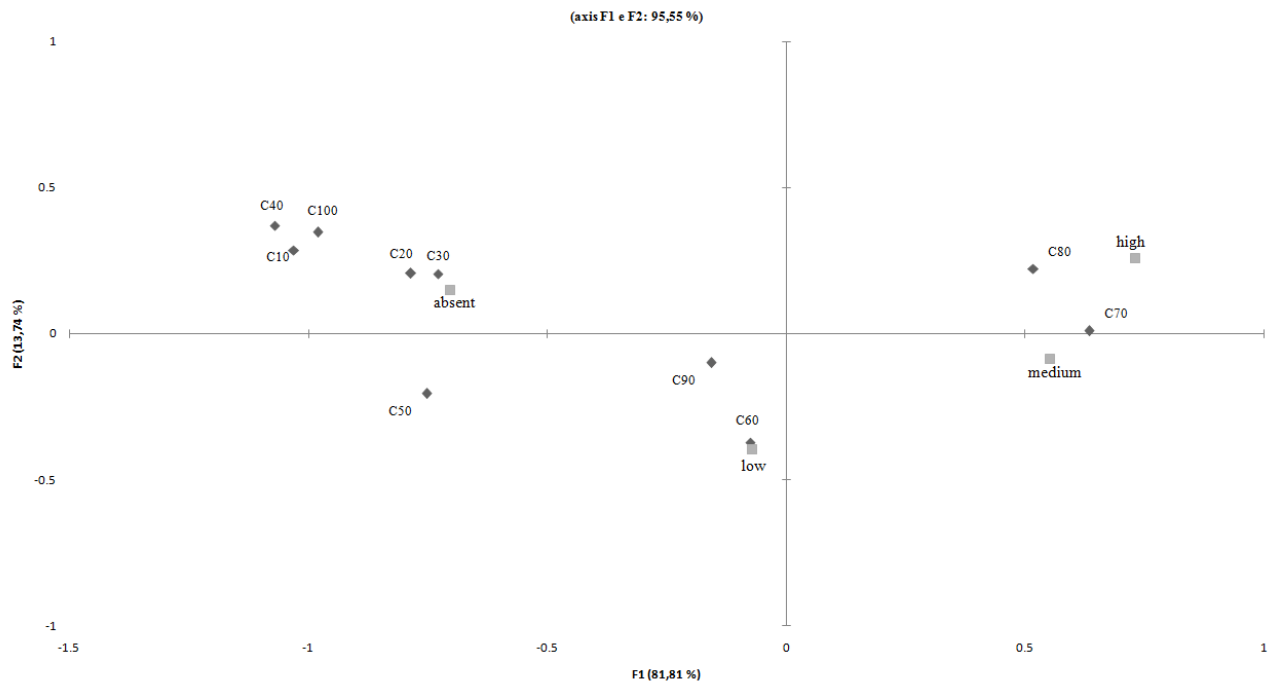
Supplementary data 3. Contour map with the distribution of *C. americanum* in the Massaguaçu River Estuary.

Canonical Correspondence Analysis between density and height of *C. americanum* and the characteristics of the Massaguaçu River estuary soil (axis F1 e F2: 100,00 %)



Supplementary data 4. Canonical Correspondence Analysis between density and height of *C. americanum* and the characteristics of the Massaguaçu River estuary soil. The relation are significative by the Monte Carlo test ($p < 0.0001$) with 1000 permutations.

Correspondence Analysis between density of *C. americanum* (high, medium and low) and the flooding classes (C10 to C100).



Supplementary data 5. Correspondence Analysis between density of *C. americanum* (high, medium and low) and the flooding classes (C10 to C100). The classes values correspond approximately to the time, in percent, that the plot stays flooded.

CAPÍTULO 5

**The effects of seasonal changing in an estuary water level over *Ludwigia octovalvis* (Jacq.)
P.H.Raven growth⁷**

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Resumo - (Efeitos da variação sazonal do nível da água de um estuário sobre o crescimento de *Ludwigia octovalvis* (Jacq)). O estuário do rio Massaguaçu é um estuário irregular, e seus ciclos da abertura de bar são irregular es e acontecem varias vezes por ano. A espécie *Ludwigia octovalvis* (Jacq) P. H. Raven (Onograceae) é perene em vários lugares do mundo, mas aparece de forma sazonal no estuário em questão. Nesse trabalho determinamos a relação entre o índice pluviométrico, o nível do estuário e a distribuição espacial e temporal dessa espécie. Em laboratório simulamos a variação do nível da água do estuário em aquários, de modo a entender como essa espécie responde ao alagamento. Em campo, determinamos a distribuição de *L. octovalvis* mais chuvosa e menos chuvosa. A espécie é relativamente comum na estação mais chuvosa, mas ausente na menos chuvosa. Existem fortes evidencias de que isso acontece devido aos ciclos de abertura de barra do inverno, mas fundos e longos, que induz essa espécie ao estiolamento, e consequentemente, a uma fragilidade mecânica. A sazonalidade de espécies em ambientes aquáticos sem uma estação biologicamente seca é incomum e pouco estudada.

Key words: ecologia de estuário, estiolamento, maré, estresse, submersão.

Abstract (The effects of seasonal changing in an estuary water level over *Ludwigia octovalvis* (Jacq)). The Massaguaçu River estuary is a irregular estuary, and its sand bar breaching cycles are irregular and happens several times each year. The species *Ludwigia octovalvis* (Jacq) P. H. Raven (Onograceae) is a perennial weed in several places around the world, but it is seasonal in the Massaguaçu River. In this survey we determined the relation between the rain, estuary water level variation, and the spatial and temporal distribution of this species. In laboratory we simulated the water level variation in water tanks in order to understand how this species responds to flooding. In the field, we determined the distribution of *L. octovalvis* in the higher pluviosty season and in the lower pluviosty season. This species is relatively common in the higher pluviosty season and completely absent in the lower pluviosty one. There are strong evidences that this happens due to the dry season longer and deeper sandbar breaching cycles, which induce this species to etiolation, and therefore, mechanical fragility. The seasonality of species in watering environments which do not have dry biological season is unusual and little studied.

Key words: etiolation, estuary ecology, stress, submergence, tidal.

1. Introduction

Plant distribution in flooded environments is mainly determined by flood frequencies, intensity and duration (Kozłowski, 1997; Sorell et al., 2002; Jackson & Colmer, 2005). Soil waterlogging triggers a variety of physic, chemical and biological changes in the soil which alter its capacity to support plant growth (Kozłowski, 1997). Plant submergence causes a reduction on the light, O₂ and CO₂ availability (Jackson & Ram, 2003), resulting in reduction of the photosynthesis. Long-term flooding can have detrimental effects even on amphibious plants (Yáñez-Espinosa et al., 2008), and re-exposure after prolonged submergence can produce toxic compounds through oxidation of the flooded soil (Biemelt et al., 1998). Submergence by moving water can also cause mechanical damage or removal of the plant from the soil. To cope with water stress, many plants developed mechanisms of tolerance or avoidance towards the soil waterlogging and shoots submergence, such as aerenchyma formation in both shoots and roots, lenticels, and timing of life cycle according the flooding conditions (Blom & Voeselek, 1996; Macek et al., 2006). Flooding also leads to changes in growth process, and shoot etiolation is a common response of submerged plants (Blom & Voeselek, 1996).

Estuarine environments, such as coastal lagoon and irregular estuaries are generally characterized by abrupt variations in their environmental conditions (Suzuki et al., 1998; Miranda et al., 2002). The breaching of the sandbar that isolates these environments from the ocean causes a drastic reduction in water level, and exposes the plants to two extremes of water supply (Macek et al., 2006). This event plays a fundamental role in estuarine fauna and flora composition (Santos et al., 2006). However, sandbar breaching and its effects on plant community is not completely established, particularly when it comes to tropical estuaries.

Massaguaçu River Estuary is a tropical irregular estuary in which, we noticed a marked seasonality in the occurrence of *Ludwigia octovalvis* (Jacq) (Onograceae) population. This species are found in summer (higher pluviosity season - HPS), but it is absent in winter (lower pluviosity season - LPS), but in our laboratory and in several other regions are perennial (Kissmann & Groth, 1997; Pott & Pott, 2000). The breaching cycles in the estuary seems to present differences between seasons, being more frequent in the HPS. We expected that *L. octovalvis* seasonality arise from this difference. To test this hypothesis our objective in the work was fourfold: (1) better characterize the differences of flooding condition between HPS and LPS, (2) determine how *L. octovalvis* respond to the different flooding conditions, (3) what is the spatial and temporal distribution of this plant in the estuary, and (4) How is the water level fluctuation related to temporal and spatial distribution of *L. octovalvis*?

2. Materials and Methods

2.1. Study species

Ludwigia octovalvis (Onagraceae) is a perennial shrubby plant that inhabits water bodies borderline, temporary lagoons, swamps and other flooded environments in the tropics (Kissmann & Groth, 1997; Pott & Pott, 2000; Francis, 2008). For over two years we cultivated this species in Federal University of São Carlos garden, both in flooded and dry soil, where species lives and flourish regardless the conditions.

2.2. Study site

The Massaguaçu River Estuary (23°37'20''S e 54°21'25''O) is an irregular estuary. Its breaching cycles are unpredictable, and range from few days to over a month. The period that the sandbar remains open is also irregular, and the connection with the ocean can last from one tidal cycle to more than two weeks. The breaching happens several times *per* year, and to the best of our knowledge there are no studies on its periodicity. According to Koeppen Classification system, the climate is tropical rain forest climate (*af*), with no pronounced winter, rain in all month, and with no biological dry season.

2.3. Estuary water level variation

We installed inside the estuary a fixed graduated scale, where zero represents the lowest level that the estuary water can reach (which occurs in the low tide when the sand bar is opened). From July 2007 to July 2008 we had daily reading of the water level. We collected pluviometric data in the Ilhabela meteorological station (2 km from the study site), and classified the year in two main seasons according to the amount of rain.

2.4. *Ludwigia Octovalvis* distribution in the estuary

In February 2008 we made a careful search in the Estuary macrophyte banks (Ribeiro et al., 2011), and plotted in a GPS the location of all points where *L. octovalvis* occur. We measured the relative high (to the graduated scale) of each point. In July 2008 we performed another search, and we also came back to check the spots previously georeferenced.

2.5. Responses to water level variation in laboratory

In a glass tank (80 cm deep, 80 cm long, 35 cm wide) we assembled four shelves, that along with the tank bottom, provided five levels 15 cm apart (respectively A, B, C, D and E from top to bottom). In each of these levels we randomly distributed five plastic pots with soil and humus (2/1) and one individual of *L. octovalvis* 7 ± 0.86 cm high. We started the experiment (day 0) with a 15 cm water column, and we gradually filled the tank so that the water level would be 30 cm on day 5, 45cm on day 10, 60 cm on day 15, 75 cm on day 20. Between day 20 and day 25 we kept the level at 75cm, and then reduced the level back to 15 cm, keeping the plants in the tank till day 30. Every five days we measured the size of each plant, and visually classified the relative size of the leaf in small, medium and big. The experiment aims to simulate the estuarine flooding condition during one breach cycles.

3. Results

3. 1. Estuary water level variation

There is no biological dry season in the study site (Walter, 1986), but there is a period when pluviosity is higher (HPS - November to April) and a period when it is smaller (LPS - from May to October). In the LPS the water level rises slower, while the bigger amount of rain makes the estuary to fill quicker. Rapid increases in water levels leads to a great number of sandbar breaching, and this event is about four times more frequent in the HPS. As the time gaps between

each breach are smaller, the oceans do not have enough time to make a higher sand bar, and the average water level in the breaching in the HPS is 28 cm lower when compared to the LPS.

3.2. *Ludwigia octovalvis* distribution in the estuary area

In the HPS we were able to find 19 spots where *L. octovalvis* occurs. The average height of these spots is 88 cm (minimum 64 cm, maximum 105 cm) above the lowest level. In the LPS scan, we were unable to find any *L. octovalvis* individue, either in the 19 spots or anywhere else.

3.3. Response to the water level variation

There were three growing patterns in the *L. octovalvis* individues: I) plants with both soil and shoots flooded during all experiment showed slow growth, and relative smaller leaves (plants from E shelf), II) plants flooded through most experiment, but with at least part of the shoots out of the water, with quicker growth, small flooded leaves and big non-flooded ones (plants from D and C shelves), and III) plants that underwent a brief flooding, with a slow growth and big leaves (plants from A and B shelves). When we removed the water, the quick-growing plants from shelves C and D were unable to support its own weight, and about 80% died. Plants from shelves A and B did not undergo an etiolation process, and still growing normally after the water removal. Plants from the shelf E etiolated in the beginning of the experiment, but soon became submerged, and its growth slowed down (Figure 1).

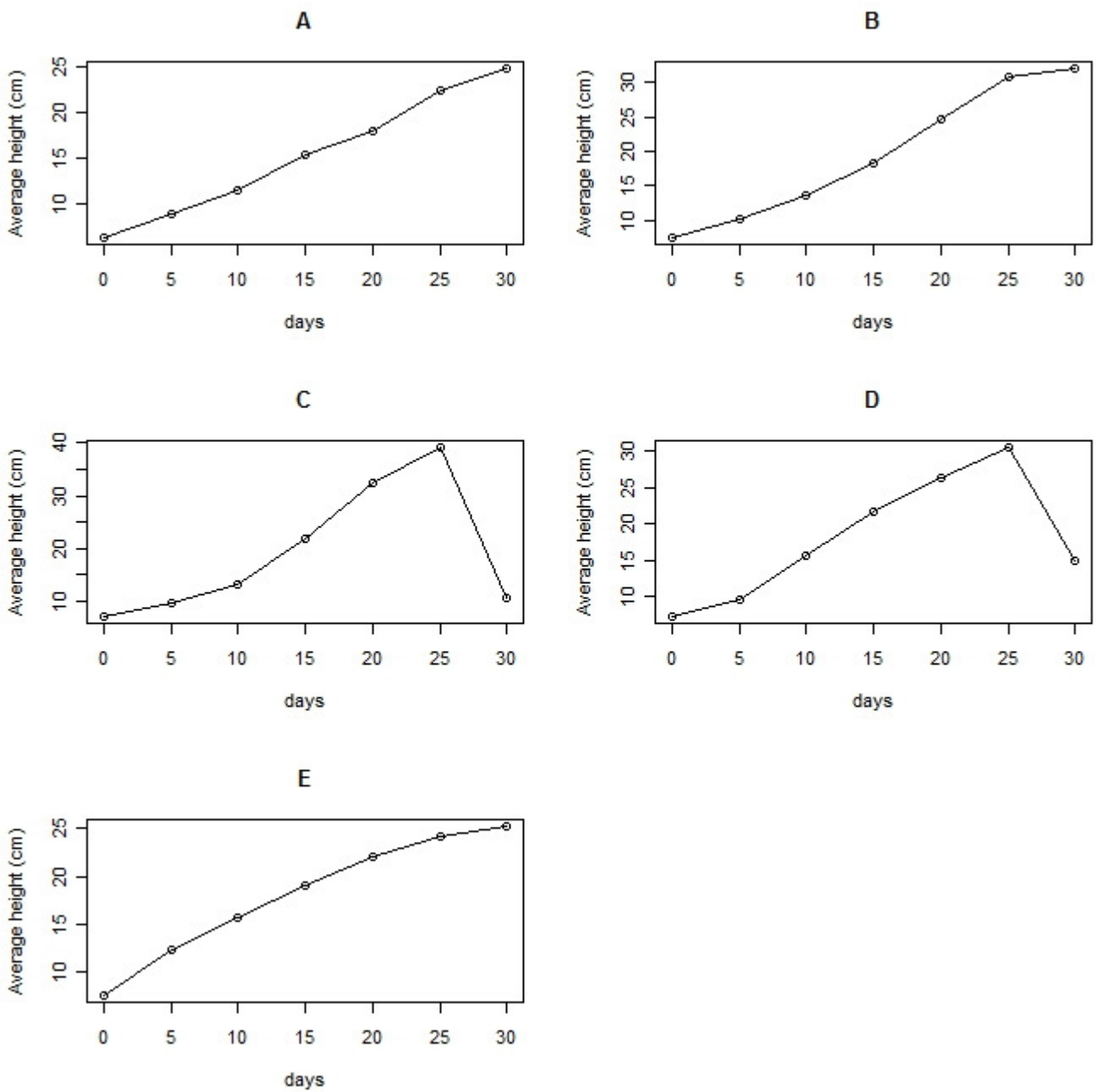


Figure 1. *Ludwigia octovalvis* (Onagraceae) individuals average size in the different flooding condition in laboratory. Dead individuals were given the value 0 cm, and negative growth values arise from that. A, B, C, D and E are the shelves.

5. Discussion

As there is a seasonal distribution of the rain, the estuary flooding cycles behave seasonally. This imposes to the organism of the estuary a seasonality that is unusual and poorly studied in aquatic environments in regions without a dry season. We believe that the seasonality presented by *L. octovalvis* arises from this process.

Crossing the average height of the spots where *L. octovalvis* occurs and estuary daily levels make it possible to quantify the flooding differences between the two seasons (Table 1). In the HPS, the *L. octovalvis* spots remain unflooded 43% of the time. This means that, when compared to the LPS, the plants have about four times more time to grow in normoxia. The HPS also presents a shorter continued submergence period, and the submerged periods are, in average, shorter. This reduces the etiolating, and allows the development of a mechanic-resistance tissue.

Table 1. Differences in the Massaguaçu river estuary flooding characteristics between the rainy and the dry season.

	Non flood period	Longest flood period	Average flooding period
rainy	43%	21 days	7.4 days
dry	10%	34 days	20.1 days

Shoot etiolation to reestablish contact with the air is a well-known response in aquatic plants (Blom & Voesenek, 1996). While etiolating plants underinvests in sustentation tissues, and become susceptible to mechanical failures (Sorell et al., 2002). The resulting botanical dry matter weights from our experiment were far below the minimum amount required by any protocol of lignin and cellulose quantification. Therefore, although highly escorted by literature, the hypothesis that the lignin production and consequent mechanical resistance are inversely proportional to *L. octovalvis* etiolation still needs to be tested. In the laboratory experiment, when the sustentation provided by the water column was removed, most of etiolated individuals either died or suffered severe injuries. In the field, it is likely that the dry season longer flooded periods induced etiolation, and therefore mechanical fragile plants. This seems to be fatal to this species when sand bar breaches and the water sustentation disappears. Thus, the flooding condition of the C and D shelves seems to be analogue to the flooding condition in the estuary during the LPS, both lead the plants to death.

In the other hand, plants from shelves A and B did not undergo shoot submersion, and the soil was only briefly flooded. This situation seems to be analogue to the one found by *L. octovalvis* individuals during the HPS, and both allow a mechanical-resistant growth.

Except for the first three days of experiments, plants from shelf E were completely submerged. The submersion of the leaves reduced the light intensity and limits the access to CO_2 , which drastically reduces photosynthesis (Jackson & Colmer, 2005), leading to a very slow growth rate. The small size at the moment the water was removed allowed the individuals from the shelf E to support its own weight, though it is very unlikely that these plants would be the competitive ones in the wild (Jackson & Colmer, 2005). Therefore, it is probable that the flooding be responsible to the absence of this species in deeper spots (spots lower than 64 cm) any time of the year. As this species is able to live in non flooded conditions, the flooding cycles cannot explain its absence in the higher spots (spots higher than 105 cm). This seems to happen due to inter-specific competition (Sorell et al., 2002), particularly competition for light, as higher spots have taller macrophytes and some trees, which may avoid enough light to reach this shade-intolerant species (Francis, 2008).

The effects of occasional water level variations are relatively well documented (Fernández-Alález et al., 1999; Riis & Hawes, 2002; Peintinger et al., 2007), and as we found in this work, there is an inverse relation between water level variation and diversity and biomass.

The artificial breaching of costal lagoons and irregular estuaries bars is a common practice in Brazil (Suzuki et al., 2002; Santos et al., 2006; Branco et al., 2007). There is a relative small number of studies regarding the impact of the breaching on estuarine communities, and they seem to have no influence in the decision of breaching manage, which is often performed by anonymous without any knowledge of the manage organ (Santos & Esteves, 2004). In the Massaguaçu River estuary, the sand bar breaching, that used to be made by fishermen or surfers, is now mainly conducted by the Caraguatatuba City Hall. The aim is to prevent flooding spots in adjacent neighborhoods. Unfortunately this is conducted without any impact studies whatsoever, and the effects of the water level management that we described to *L. octovalvis* will certainly reaches other flora and fauna species.

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CONSIDERAÇÕES FINAIS

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Durante a realização desse doutorado, um fato sempre me chamou a atenção: a absoluta falta de paralelos na bibliografia. Durante muito tempo, atribuí a ausência de outros trabalhos relacionados aos padrões de distribuição vegetal e aos mecanismos por trás desses padrões simplesmente à minha incompetência em localizá-los. Com o tempo, eu fui percebendo que de fato esses trabalhos não existiam, e que o nosso grupo de pesquisa foi o primeiro a realizar trabalhos desse cunho em um estuário tropical irregular. Por um lado, isso foi uma das grandes dificuldades da realização desse doutorado, uma vez que frequentemente não tínhamos o escoro de uma referência. Por outro, isso o tornou extremamente estimulante, primeiro porque exigiu a criação e a adaptação de várias metodologias, e segundo porque nos permitiu chegar a resultados que, sob muitos aspectos, são inéditos.

Ao mesmo tempo em que o conjunto de trabalhos apresentados nessa tese representa um avanço no conhecimento sobre o Estuário do Rio Massaguaçu, eles levantam um série de perguntas: como esses processos acontecem em outros estuários tropicais irregulares? Até que ponto as informações obtidas nesse trabalho podem ser extrapoladas para outros estuários?

Eu nunca gostei de terminar um trabalho com a frase: “mais estudos precisam ser realizados”. Há quem diga que a ciência é incapaz de responder a uma pergunta sem fazer outra, mas isso sempre me pareceu uma resposta simplista de um trabalho feito com menos esmero que o necessário. Queimando a minha língua – coisa que tenho feito com certa frequência - hoje eu acredito que a minha mais sincera conclusão é a necessidade de avançar os estudos, replicando trabalhos com esse enfoque em outros estuários, no sentido de entender esses ambientes de uma maneira mais ampla.